AD-A212 287

Electrophysiological Studies of Visual Attention

and Resource Allocation

(Final Report)

Principal Investigator: Steven A. Hillyard

Department of Neurosciences

University of California, San Diego

La Jolla, California   92093-0608

REPORT DOCUMENTATION PAGE

Form Approved
OMB No 0704-0188

1a REPORT SECURITY CLASSIFICATION		1b RESTRICTIVE MARKINGS
Unclassified		N. A.

2a SECURITY CLASSIFICATION AUTHORITY	3 DISTRIBUTION / AVAILABILITY OF REPORT
N. A.	Approved for public release;
2b DECLASSIFICATION / DOWNGRADING SCHEDULE	distribution unlimited.
N. A.	

4. PERFORMING ORGANIZATION REPORT NUMBER(S)	5 MONITORING ORGANIZATION REPORT NUMBER(S)
SDEPL 002	Same

6a NAME OF PERFORMING ORGANIZATION Dept of Neuroscience U. California, San Diego	6b OFFICE SYMBOL (If applicable)	7a NAME OF MONITORING ORGANIZATION Office of Naval Research

6c. ADDRESS (City, State, and ZIP Code) La Jolla, CA 92093-0608	7b ADDRESS (City, State, and ZIP Code) 800 N. Quincy Street Arlington, VA 22217-5000

8a. NAME OF FUNDING / SPONSORING ORGANIZATION Office of Naval Research	8b OFFICE SYMBOL (If applicable) Code 1142PS	9 PROCUREMENT INSTRUMENT IDENTIFICATION NUMBER N00014-86-K-0291

8c. ADDRESS (City, State, and ZIP Code) 800 N. Quincy Street Arlington, VA 22217-5000	10 SOURCE OF FUNDING NUMBERS			
	PROGRAM ELEMENT NO	PROJECT NO	TASK NO	WORK UNIT ACCESSION NO
	61153N 42	RR04209	RR0420901	R&T4426556

11 TITLE (Include Security Classification)
(U)
Electrophysiological Studies of Visual Attention and Resource Allocation

12 PERSONAL AUTHOR(S)
S.A. Hillyard, G.R. Mangun and S.J. Luck

13a TYPE OF REPORT Technical/Final	13b TIME COVERED FROM 86/06/01 TO 89/05/31	14 DATE OF REPORT (Year, Month, Day) August 15, 1989	15 PAGE COUNT 48

16 SUPPLEMENTARY NOTATION
30

17	COSATI CODES		18 SUBJECT TERMS (Continue on reverse if necessary and identify by block number)
FIELD	GROUP	SUB-GROUP	Selective attention, visual system physiology, spatial orienting, event-related brain potentials

19 ABSTRACT (Continue on reverse if necessary and identify by block number)

The objective of this project has been to better understand mechanisms of visual selective attention in humans, both at the level of perceptual processing and at the level of the underlying brain mechanisms. The main approach has been to record event-related brain potentials (ERPs) from the intact scalp using multielectrode arrays. Selective attention to stimulus location was found to enhance short-latency brain evoked activity, and analysis of current source densities indicated that visual inputs were subject to attentional control at or before the level of the pre-striate occipital cortex. Similar patterns of early sensory modulation were found during spatially focussed attenton to rapid sequences of unilateral stimuli, to single stimuli occurring at precued locations, and to bilateral stimulus arrays. Applications of these techniques for evaluating how human operators allocate their attention to visual displays are discussed.

20 DISTRIBUTION / AVAILABILITY OF ABSTRACT ☒ UNCLASSIFIED/UNLIMITED ☒ SAME AS RPT ☐ DTIC USERS	21 ABSTRACT SECURITY CLASSIFICATION Unclassified
22a NAME OF RESPONSIBLE INDIVIDUAL Teresa A. McMullen	22b TELEPHONE (Include Area Code) (202) 696-3163	22c OFFICE SYMBOL Code 1142PS

DD Form 1473, JUN 86   *Previous editions are obsolete*   SECURITY CLASSIFICATION OF THIS PAGE

S/N 0102-LF-014-6603

89 9 12 086

Objectives

The principal objective of this project has been to better understand mechanisms of visual selective attention in humans both at the level of perceptual processing and at the level of the underlying brain mechanisms. The primary experimental approach is the recording of event-related brain potentials (ERPs) from the intact scalp using multi-electrode arrays. The ERPs are voltage oscillations triggered by sensory stimuli that represent the summated electric fields arising from neuronal activity patterns in the afferent pathways and cortical areas engaged in processing the stimulus information. The successive waves or "components" of the human visual ERP are characterized by a latency that indicates the timing of the underlying neural activity, a localization on the scalp determined by the geometry of the active neural tissue, and an amplitude determined by the net synaptic activity in the neuronal generator population (Hillyard and Picton 1987). By studying how selective attention affects specific early and late ERP components, conclusions may be reached about which stages of sensory processing are modulated by attention, which types of sensory information are being enhanced or suppressed, and which brain areas participate in the attentional control processes.

This project has concentrated on analyzing mechanisms of visual spatial attention. Human observers have a remarkable capability for deploying their attention rapidly to the critical regions of a visual scene or display in order to extract the information in an optimal fashion. A rapidly expanding research literature has established that stimuli occurring at or near an attended location are processed more efficiently than are stimuli at some distance from the focus of attention; this enhanced processing may take the form of improved detectability for faint stimuli, improved discriminability of stimulus features and patterns, or speeded motor responses to expected targets (reviewed in Ericksen and Yeh 1985; Prinzmetal et al., 1986; Downing 1988).

A major goal of our project has been to determine whether moving attention to a location results in an improvement of the quality of sensory information that is taken in as opposed to a change in the decision criterion for responding to the attended events. This is a version of the traditional "early" versus "late" selection issue--does attention actually modulate the flow of sensory information at a relatively early level of processing or does it bias higher recognition and decision stages to favor specific inputs? As described below, our finding that short-latency (80-100 msec) ERP components localized to visual cortex are enhanced by spatial attention lends support to the view that information is being gated at the level of sensory processing.

In addition to investigating basic mechanisms of attention, another goal has been to develop ERP measures as indices of attentional allocation to visual displays. An advantage of the ERP method in this regard is that the distribution of attention among the elements of a display can be assessed without requiring any overt motor response from the subject. Thus, the relative amount of attention being paid to multiple elements in the field, both relevant and irrelevant, can be measured unobtrusively without requiring a behavioral response to each class of stimulus event. Such response requirements may in themselves disturb the pattern of attentional allocation away from the principal task at hand. Based on these considerations, our ERP results have applications in the design and evaluation of visual displays and in the on-line monitoring of observer performance/effectiveness in operational environments. As described below, we have recently made a significant advance in this area by showing that the ERPs can index the lateralized focussing of attention <u>within</u> a circumscribed zone of a bilaterally symmetrical display. This means that the ERP method can be applied to a broad class of display contexts in which information is presented simultaneously throughout the visual field.

General Approach

Our basic ERP approach is illustrated in Fig. 1 (Mangun and Hillyard in press). Stimuli are presented unpredictably to specified locations in the right or left visual field, and one of the fields is designated as relevant (either on a trial-by-trial basis or for an entire block of stimuli, depending on task design.). The subject is required to maintain fixation on a central point while discriminating the stimuli at the attended location and ignoring stimuli at the unattended location.

In Figure 1, the stimuli are flashed bars on a video screen, occuring on a random basis either 5 degrees to the right or left of fixation, with inter-stimulus intervals randomized between 250-500 msec. The subject's task is to attend to and discriminate the height of the bars at one location (ignoring the other location) and to press a button upon detecting slightly shorter (target) bars occurring 10% of the time. Attention is sustained to one location over runs lasting 1-2 mi. es.

The occipital ERP to these flashed bars consists of a series of prominent voltage peaks or components, including P1 (100-135 msec, N1 (160-190 msec), P2 (220-250 msec) and N2 (260-290 msec) waves. The ERPs shown are in response to left-field flashes, and the earliest components (P1 and N1) have narrowly focussed scalp distributions over the visual cortex contralateral to the field of stimulation in accordance with the anatomical layout of the visual pathways. The effect of attending to the left field flashes is seen to be an enhancement of the P1, N1 and N2

amplitudes (an equivalent enhancement of the ERPs to right field flashes occurs when attention is directed to the right--not shown in Figure 1).

Note: The same pattern of P1-N1 enhancement is seen for <u>all</u> stimuli flashed at an attended location, targets and non-targets alike. Only non-target ERPs are shown in these Figures. Targets waveforms would include later N2 and P300 component which reflect the subjects' correct detection of the task-relevant stimulus.

The waveform properties of these attention-related changes provide information as to the physiological mechanisms of spatial attention. First, the fact that attention is reflected in the earliest observable occipital component (the P1, which onsets as early as 70-75 msec depending on stimulus brightness and eccentricity) indicates that selection for location begins to affect processing at an early stage in the visual pathways. Second, the fact that the attentional change is one of amplitude modulation with no alteration in waveform or scalp distribution indicates the operation of a <u>sensory gain control</u> mechanism at an early stage in the visual pathways. Thus, spatial attention seems to exercise an early input control over the flow of sensory information to higher levels of the visual system, with a relative suppression of inputs from unattended locations (Mangun and Hillyard 1987; 1988; in press).

<u>Localization of Cortical Locus of Attentional Control</u>

In recent studies, we have obtained more precise localization of the attention-sensitive P1 wave by means of 32-channel scalp recordings supplemented by current source density (CSD) analyses. The CSD is calculated as a second spatial derivative transform of the voltage gradients on the scalp, which provides an estimate of the instantaneous electrical currents that are flowing from the brain perpendicularly to the surface at that scalp location (MacKay 1984; Mitzdorf 1985). The two-dimensional CSD distribution over the scalp is obtained by placing electrodes in a geometrical grid such that each electrode sits in the center of a square comprised of four neighboring electrodes (i.e., a LaPlacean montage); the second derivative CSD is given by subtracting the average voltage of the four surrounding electrodes from that of the central electrode. By mapping the distribution of the perpendicular currents over the electrode array, the neural generators producing the current flows can be localized within the underlying cortical areas. The CSD analysis is better suited to localizing cortical generators than is simple voltage mapping, since the current flow calculations are reference-free and specifically emphasize superficial rather than deep generator sources (Srebro 1987; Pernier <u>et al.</u>, 1988).

A comparison of voltage mappings and the derived CSD mappings is shown in Fig. 2 for the P1 component (100-120 msec) elicited by small rectangular flashes of light in the upper left and right quadrants of the visual field. In this experiment, rectangles were flashed to the four quadrants of the visual fields (ca. 6 degrees from fixation) in random order at interstimulus intervals of 250-450 msec. The subject's task was to attend selectively to the stimuli at one of the four locations and to press a button upon detecting infrequent "target" stimuli (slightly smaller rectangles) at that location. As is usual in this type of experiment, the flashes at attended locations elicited an enlarged P1 component that did not change in waveshape or scalp distribution in relation to when the flashes were unattended.

The CSD maps in the lower portion of Fig. 2 show the current densities over a grid of 12 LaPlacean electrode arrays situated over the posterior scalp. A sharply focussed current source for the P1 wave to attended-flashes is seen over the occipital lobe contralateral to the field of stimulus presentation. A smaller source can be seen in the mirror-image position of the ipsilateral hemisphere, which probably represents transmission of evoked activity across the corpus callosum, since that source appears 15-20 msec later than the principal, contralateral source.

The localization of the P1 generator in relation to cortical areas can be visualized better by superimposing the CSD map over a lateral view of the cerebral hemispheres (Figure 3). This mapping is based on averaged P1 topographic data from eight subjects and uses the data of Homan et al. (1987) for correlating scalp electrode sites with underlying cortical areas. It can be seen that the focus of P1 activity is over the ventral-lateral prestriate cortex (Brodmann's areas 18-19), which suggests that spatial attention acts to modulate the flow of information between primary visual cortex and the higher cortical areas (V4 and inferior temporal lobe) that analyze form and color information.

In monkeys, the ventral-lateral prestriate cortex includes areas V2, VP, and V4, which analyze form and color information received from striate cortex and project outputs to inferior temporal cortex (DeYoe and Van Essen 1988). There are some intriguing correspondences between the human P1 component and the neural activity recorded from area V4 in monkeys. The latencies of V4 units in macaques range from 70-90 msec (Robinson & Rugg 1988), which is in line with the P1 onset latencies of 80-100 msec (depending on stimulus brightness and eccentricity). In addition, Desimone and associates have found that unit activity in the monkey area V4 (but not areas V1 or V2) is sensitive to whether or not attention is being paid to the location of the evoking stimulus (Moran & Desimone 1985; Spitzer et al., 1988). Thus we would tentatively propose that the P1 amplitude variations observed in our spatial attention paradigms may represent

the attentional control of information transmission through the human homologue of visual area V4. On the basis of present evidence, however, we cannot rule out the possibility that the P1 variations manifested over prestriate areas may be actually imposed at an earlier level of the visual pathway. Further work is needed to bring these lines of research in humans and monkeys together.

II: Attentional Allocation with Bilateral Stimulus Arrays

In previous work we showed that the P1 and N1 components were sensitive indices of the controlled allocation of attention to unilateral arrays of letters flashed briefly to the left and right visual fields (Mangun and Hillyard 1987; 1986; Hillyard and Mangun in press). Both P1 and N1 amplitudes increased montonically as more attention was allocated to the stimuli in a particular visual field, and ERP amplitudes correlated closely with attention-related increases target detectability. In the studies outlined below, we have extended this work to task situations in which bilaterally symmetrical stimulus arrays were flashed on a screen and subjects had to attend to a restricted portion of the displays in the right or left visual field.

This bilateral stimulus design was investigated: (1) because stimulus arrays of this type allow a high degree of attentional selectivity in behavioral priming studies, (2) because of its relevance to visual displays in operational environments, and (3) because it enabled us to test our hypothesis that the P1 wave reflects an early sensory gain control process during spatially focussed attention (for a more detailed rationale of these studies, see Hillyard et al., in press; Heinze et al., in press).

In the study of Heinze et al. (in press), we presented subjects with briefly flashed arrays of 4 letters, 2 in each visual field, situated 3-5 degrees lateral to fixation (See Fig. 4). These arrays were delivered at a rate of 2/second, and the subject was instructed to attend to the letter pair in one field at a time and to push a button in response to those occasional arrays where the two letters in the attended field were identical (targets). This task produced a highly selective attentional state, such that subjects had no awareness of what letters were presented in the unattended field.

The ERPs to those bilateral letter arrays (Fig. 5, shows ERPs to non-targets) shows the P1 component (80-150 msec) to be enhanced over the occipital cortex contralateral to the attended visual field. In Figure 5, ERPs from right and left temporal (T5/6) and occipital (01/2) scalp sites were collapsed together according to whether attention was directed to the visual field ipsilateral vs. contralateral to the recording site. The

contralateral enhancement of the P1 is consistent with the hypothesis that spatially focussed attention acts to facilitate visual information coming from the attended location, whether the attended stimulus is presented unilaterally (as in previous studies) or is part of a larger, bilateral complex. This shift in P1 asymmetry to the contralateral hemisphere can be seen more clearly in the voltage topographical maps over the head of the the P1 elicited by bilateral, non-target arrays (Fig. 6): when attention was directed to the left letter pair, the P1 was larger over the right occipital cortex, and vice versa.

An even stronger index of lateralized attention was seen in the ERPs to the irrelevant "probe" flashes (Fig. 4, frame 4) that were flashed at random to either the right or left field. These rectangular flashes had nothing to do with the letter match task and did not disrupt it, but the P1 amplitude to the probes was greatly enlarged for probes presented to the attended versus unattended visual field (Fig. 7). This finding strongly supports the hypothesis that the P1 amplitude modulation reflects an early visual pathway faciliation, which enhances responses to task irrelevant rectangular flashes as well as to task-relevant letters. The strong spatial selection in this task was also manifested in the complete suppression of the subsequent "N2" wave (250 msec) associated with detection of task relevant targets for letter pairs in the unattended visual field (see Heinze et al., in press; Luck et al., in press).

Application: The finding that irrelevant probe ERPs are enlarged when the probes fall in an attended zone of visual space has important applications for studying how subjects allocate attention to visual displays. Based on our current results, it would be entirely feasible to set up a display (such as an instrument panel) in which all the locations where information appears are stimulated from time to time with irrelevant probe stimuli and ERPs are recorded. In this way one could assess whether the subject is maintaining a focussed state of attention, and what proportion of his or her attentional resources are being allocated to the various elements of the display, even during periods when no overt responses are produced.

A further set of studies (described in Hillyard et al., in press) was designed to examine the perceptual correlates of the focussing of attention to one half of a bilateral display. In this design, bilateral arrays of "nonsense" symbols were flashed in a rapid, random sequence. These symbols were chosen to eliminate the automatic perceptual recognition associated with letter or number stimuli. The subject's task was to focus attention to one side of the display and to observe each stimulus pair on that side so they could make a match/mismatch judgement with respect to a unilateral "probe" pair of symbols that occurred occasionally and unpredictably on either side.

As in the previous study, the probe (a relevant probe in this case) elicited a much larger P1 component when it occurred on the side where attention was focussed. Correlated with this P1 enhancement was a marked improvement in d' for matching the probe against the immediately preceding symbol pair in the attended field. These data indicate that focussing attention on one location within a bilateral display results in a relative improvement/degradation of information presented to attended/unattended portions of the display, which is indexed by a relative enhancement/suppression of the P1 wave over the contralateral visual cortex.

III: Overview of ERPs and Spatial Selective Attention

The studies supported by this contract have shown that the same pattern of early ERP facilitation (manifested in an enhanced P1 wave) is produced by spatially focussed attention in several different experimental contexts including: (1) sustained attention to one sequence of randomized unilateral stimuli while ignoring another (Mangun and Hillyard 1987, 1988; (2) trial by trial cueing of attention to a location where a unilateral stimulus is expected (Posner paradigm, Figs. 8 and 9) (Mangun et al., 1987); (3) sustained attention to one field while bilateral stimuli and unilateral probes are presented (Heinze et al., in press; Luck et al., in press). In each case, the stimulus or stimulus element falling upon the attended location elicits an enlarged P1 wave over the contralateral occipital scalp. The hypothesis that the spatial focussing of attention results in an early, non-stimulus-specific, boost of sensory information arising from the attended location is strongly supported by these data and is congruent with behavioral studies showing an improvement in d' for detecting and recognizing attended-location stimuli (Downing 1988).

IV: Appended Manuscript

A more detailed presentation of some of the above discussed results is given in the appended manuscript:

Electrophysiology of Visual Attention

(S.A. Hillyard, G.R. Mangun, S.J. Luck and H.J. Heinze)

Prepared for Conference on Machinery of Mind

To be published by Birkhausen, Boston.

References

1. DeYoe, E.A. and D.C. VanEssen. Concurrent processing streams in monkey visual cortex. <u>Trends</u> <u>in</u> <u>Neuroscience</u>, <u>11</u>, 219-226, 1988.

2.   Downing, C.J.   Expectancy and visual-spatial attention: Effects on perceptual quality. <u>J</u>. <u>Exper</u>. <u>Psychol</u>.:<u>Hum</u>. <u>Percept</u>. <u>Perf</u>. <u>14</u>, 188-202, 1988.

3. Eriksen, C.W. and Y.Y. Yeh. Allocation of attention in the visual field.   <u>J</u>. <u>Exper</u>. <u>Psychol</u>.: <u>Human</u> <u>Percept</u>. <u>and</u> <u>Perf</u>. <u>11</u>: 583-597, 1985.

4. Heinze, H.J., S.J. Luck, G.R. Mangun and S.A. Hillyard. Visual event-related potentials index focussed attention within bilateral stimulus arrays: I.   Evidence for early selection. <u>Electroenceph</u>. <u>clin</u>. <u>Neurophysiol</u>. In Press.

5. Hillyard, S.A., G.R. Mangun, S.J. Luck and H.J. Heinze. Electrophysiology of visual attention.   In: E.R. John <u>et</u> <u>al</u>., (Eds.). Proceedings of Conference on <u>Machinery</u> <u>of</u> <u>Mind</u>. Bir-khausen, Boston. In Press.

6. Hillyard, S.A. and T.W. Picton. Electrophysiology of cogni-tion. In: F. Plum (Ed.). <u>Handbook</u> <u>of</u> <u>Physiology</u> <u>Section</u> <u>1</u>: <u>The</u> <u>Nervous</u> <u>System</u> <u>Vol</u>. <u>V</u> <u>Higher</u> <u>Functions</u> <u>of</u> <u>the</u> <u>Brain</u>. Part 2 American Physiological Society. 1987, pp. 519-584.

7. Homan, R.W., J. Herman and P. Purdy. Cerebral location of international 10-20 system electrode placement. <u>Electroenceph</u>. <u>clin</u>. <u>Neurophysiol</u>., <u>66</u>, 376-382, 1987.

8. Luck, S.J., H.J. Heinze, G.R. Mangun and S.A. Hillyard. Visual event-related potentials index focussed attention within bilateral stimulus arrays: II. Functional dissociation of P1 and N1 components. <u>Electroenceph</u>. <u>clin</u>. <u>Neurophysiol</u>. In Press.

9. MacKay, D.M. Source-density mapping of human visual recep-tive fields using scalp electrode. <u>Exper</u>. <u>Brain</u> <u>Res</u>., <u>54</u>, 579-581, 1984.

10. Mangun, G.R., J.C. Hansen and S.A. Hillyard. Electroretino-grams reveal no evidence for centrifugal modulation of retinal inputs during selective attention in man.   <u>Psychophysiology</u> <u>23</u>: 156-165, 1986.

11.   Mangun, J.C. Hansen and S.A. Hillyard. The spatial orient-ing of attention: Sensory facilitation or response bias? In: R. Johnson, J. Rohrbaugh and R. Parasuraman (Eds.). <u>Current</u> <u>Trends</u> <u>in</u> <u>Event</u>-<u>Related</u> <u>Potential</u> <u>Research</u>. <u>Electroenceph</u>. <u>clin</u>.

Neurophysiol. Suppl. 40: 118-124, 1987.

12. Mangun, G.R. and S.A. Hillyard. The spatial allocation of visual attention as indexed by event-related brain potentials. Hum. Fact. 29: 195-211, 1987.

13. Mangun, G.R. and S.A. Hillyard. Spatial gradients of visual attention: Behavioral and electrophysiological evidence. Electroenceph. clin. Neurophysiol. 70: 417-428, 1988.

14. Mangun, G.R. and S.A. Hillyard. Electrophysiological studies of visual selective attention in humans. In: A. Scheibel and A. Wechsler (Eds.). The Neurobiological Foundations of Higher Cognitive Function. Guilford, New York. In Press.

15. Mitzdorf, U. Current source-density method and application in cat cerebral cortex: Investigation of evoked potentials and EEG phenomena. Physiol. Rev. 65, 37-100, 1985.

16. Moran, J. and R. Desimone. Selective attention gates visual processing in the extrastriate cortex. Science, 229, 782-784, 1985.

17. Pernier, J., F. Perrin and O. Bertrand. Scalp current density fields: Concept and properties. Electroenceph. clin. Neurophysiol., 69, 385-389, 1988.

18. Prinzmetal, W., D.E. Presti and M.I. Posner. Does attention affect visual feature integration? J. Exper. Psychol.: Hum. Percept. Perform. 12: 361-369, 1986.

19. Robinson, D.L. and M.D. Rugg. Latencies of visually responsive neurons in various regions of the Rhesus monkey brain and their relation to human visual responses. Biol. Psychol., 26, 111-116, 1988.

20. Spitzer, H., R. Desimone and J. Moran. Increased attention enhances both behavioral and neuronal performance. Science, 240, 338-340, 1988.

21. Srebro, R. The topography and scalp potentials evoked by pattern pulse stimuli. Vision Res., 27, 901-914, 1987.
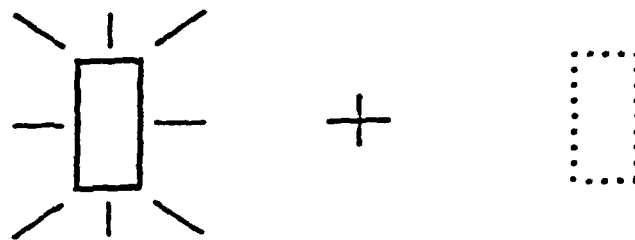
Scalp
Topography
of P1 Wave
(133 msec)
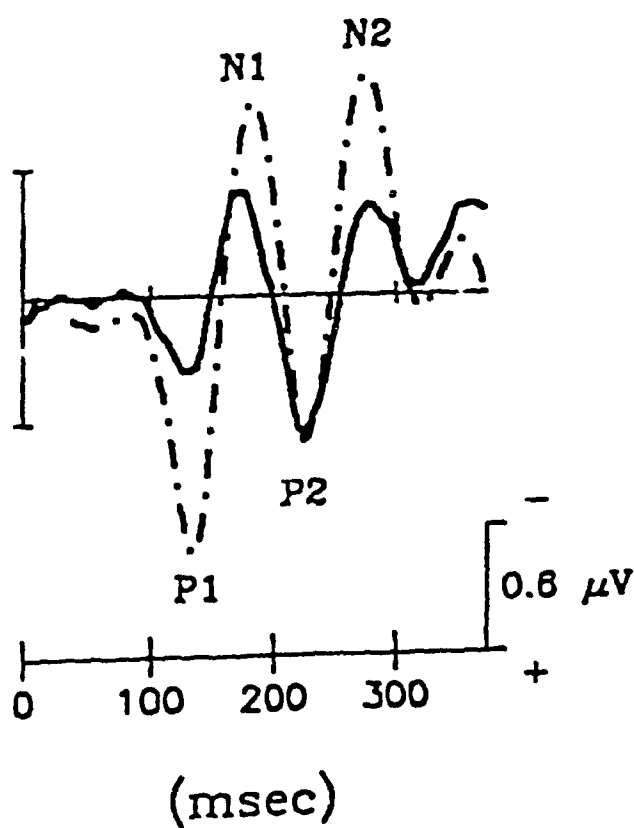
Amplifiers
Signal Averager

ERPs
to
Left Flashes

N1
N2
P2
P1
0.6 μV
−
+

0   100   200   300

Attend Left
— · — · —

Attend Right
———

(msec)

Fig. 1

P1 SCALP TOPOGRAPHY (108 ms)

Left Flashes   Right Flashes

Voltage

CSD

uV

uV/cm²
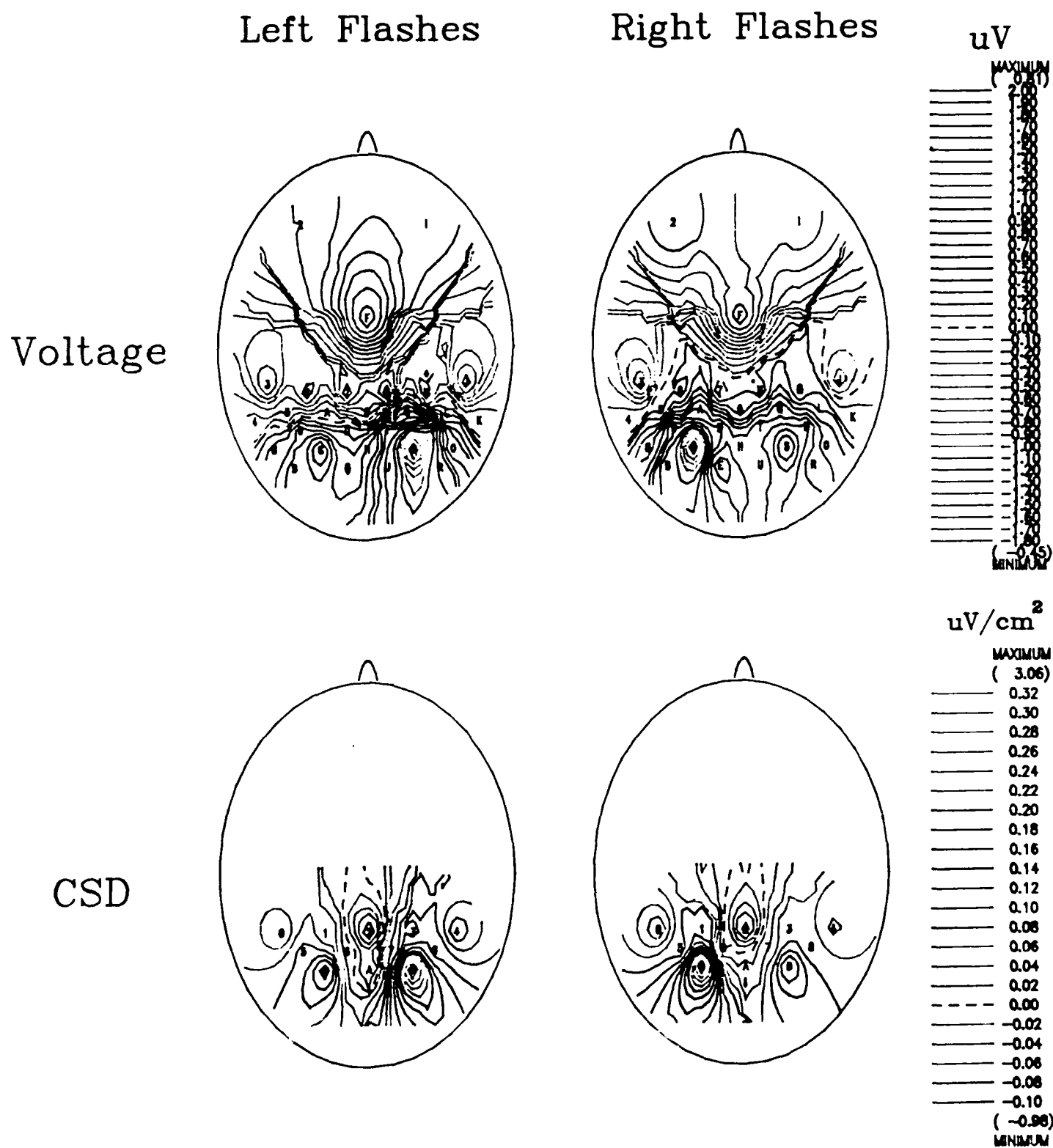
Fig. 2

P1–CSD TOPOGRAPHY (108 ms)
RIGHT FIELD FLASHES

Fig. 3

1 | É F́ + É T́

2 | T́ É + F́ F́

3 | É É + Ĺ T́

4 | ▯ +

5 | T́ Ĺ + F́ Ĺ

Fig. 4

BILATERAL NON-TARGETS

T5/6

O1/2

N1

P1

Contra

·············· Ipsi

1.0 μV

0   200   400
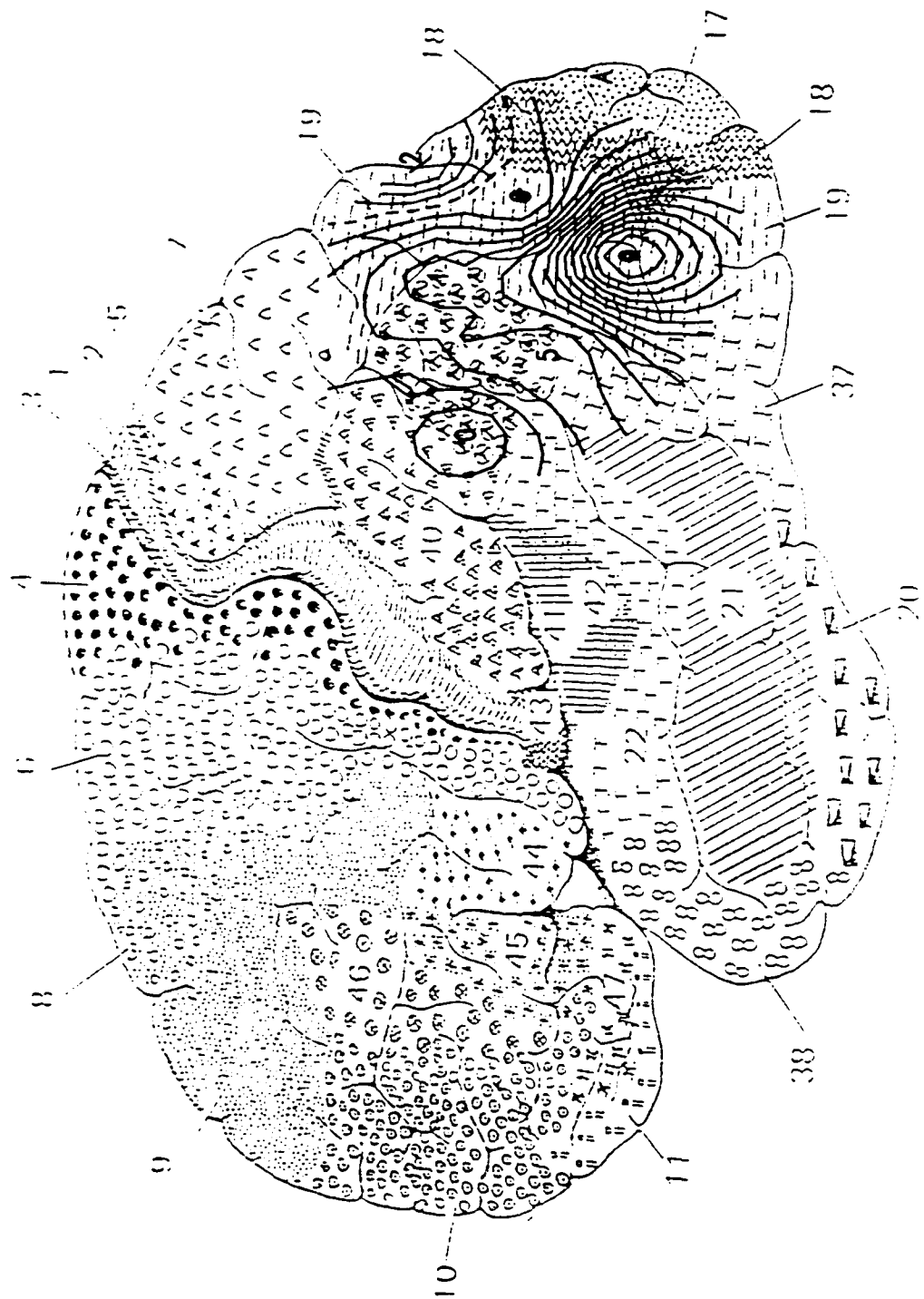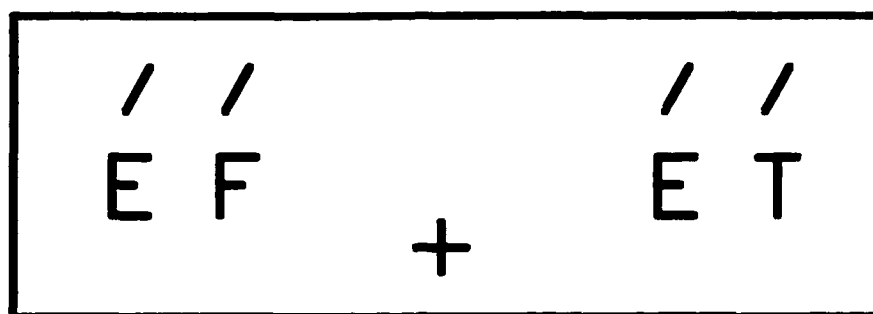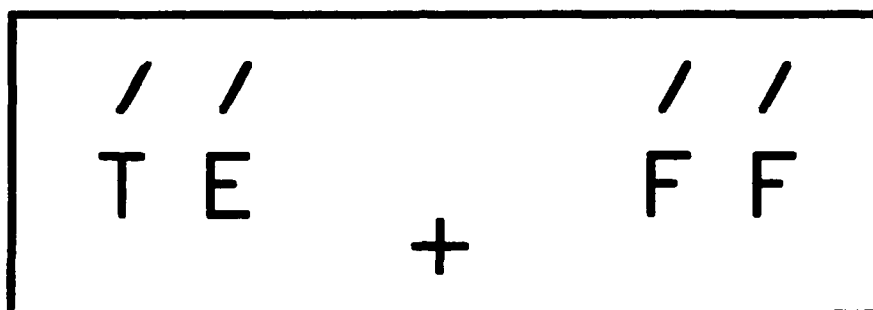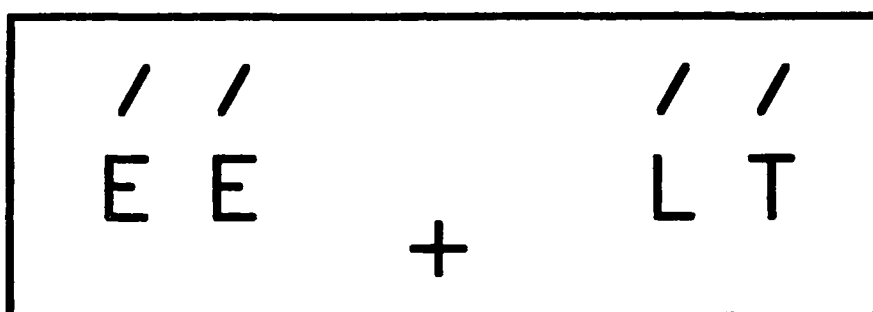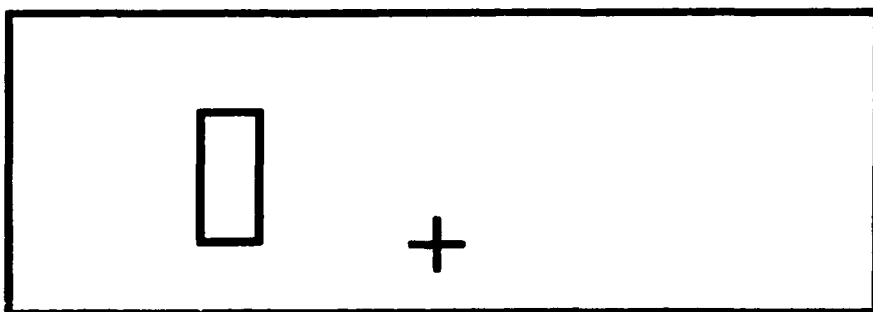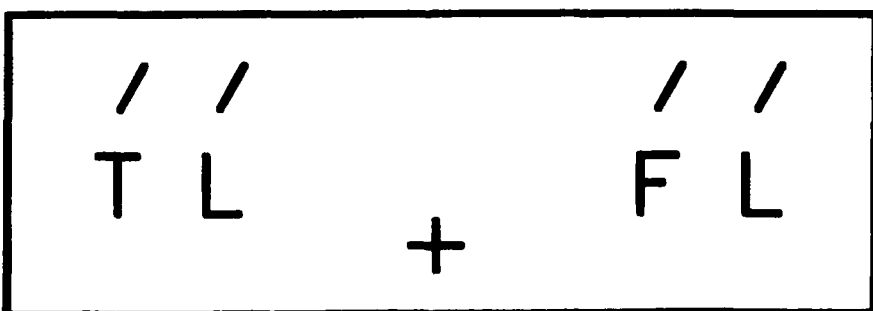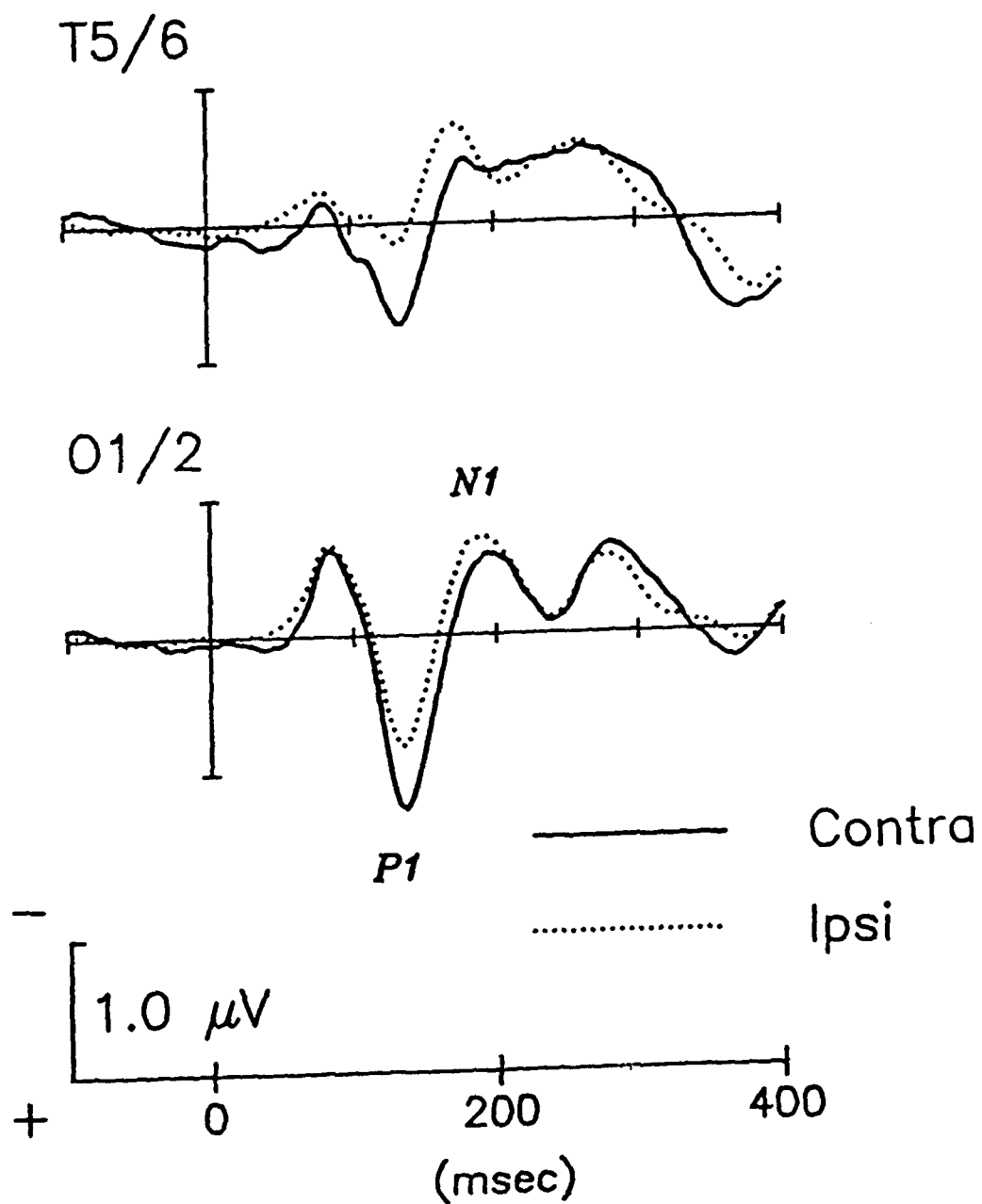
(msec)

Fig. 5

SCALP TOPOGRAPHY OF P1

Attend Right

110 msec
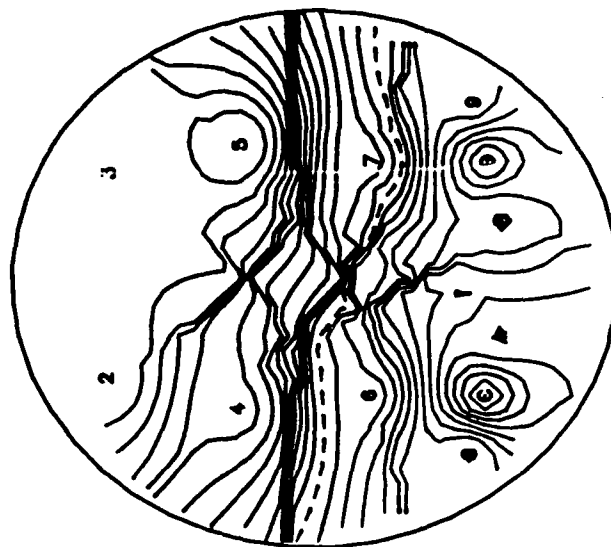
Bin 16 in File gr.c
Bilat standards cd 2 before unilat
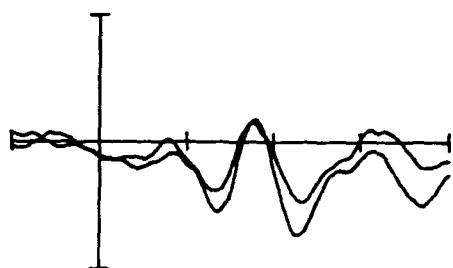attend right
GR.SWITCH
MI Unilat Switching

MAXIMUM
(1.00)
1.05
0.97
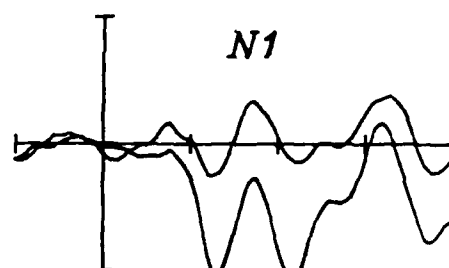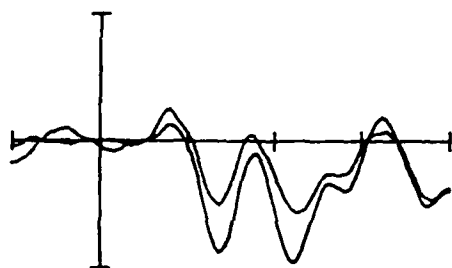0.90
0.82
0.75
0.67
0.60
0.52
0.45
0.38
0.30
0.22
0.15
0.07
0.00
-0.07
-0.15
-0.22
-0.30
-0.38
-0.45
-0.52
-0.60
-0.67
-0.75
-0.82
-0.90
-0.97
-1.05
(-1.07)
MINIMUM

Attend Left

110 msec

Bin 4 in File gr.c
Bilat standards cd 1 before unilat
attend left
GR.SWITCH
MI Unilat Switching

Fig. 6

ERPS TO BAR PROBES
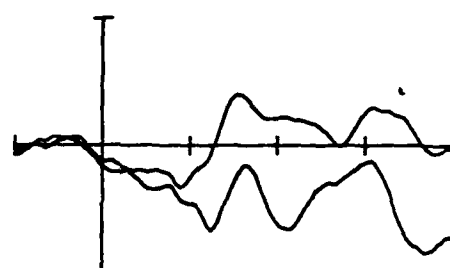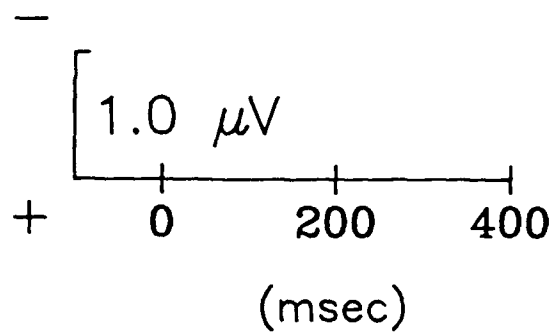
Fig. 7

CHOICE RT – POSNER PARADIGM
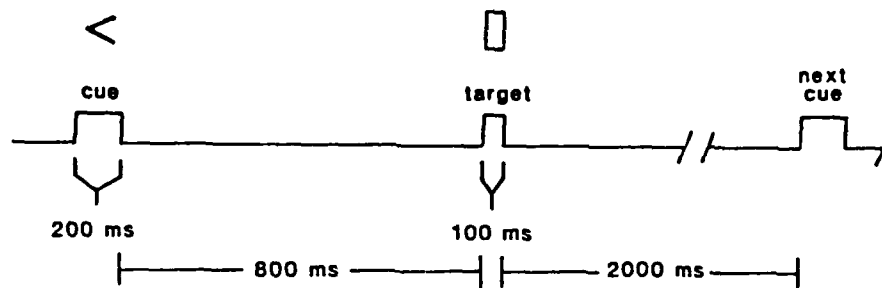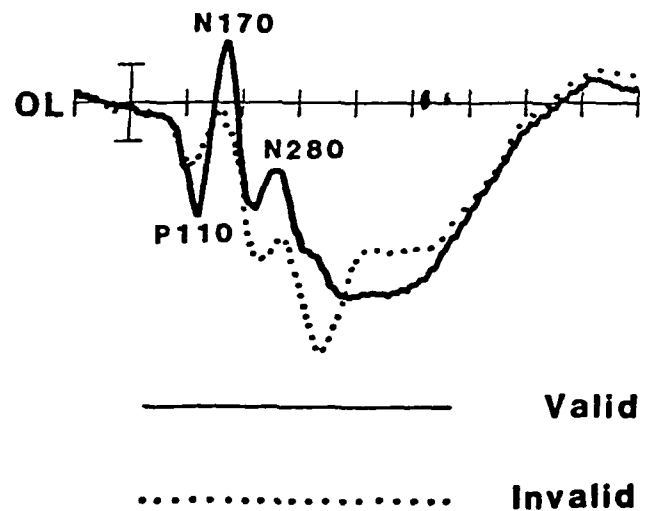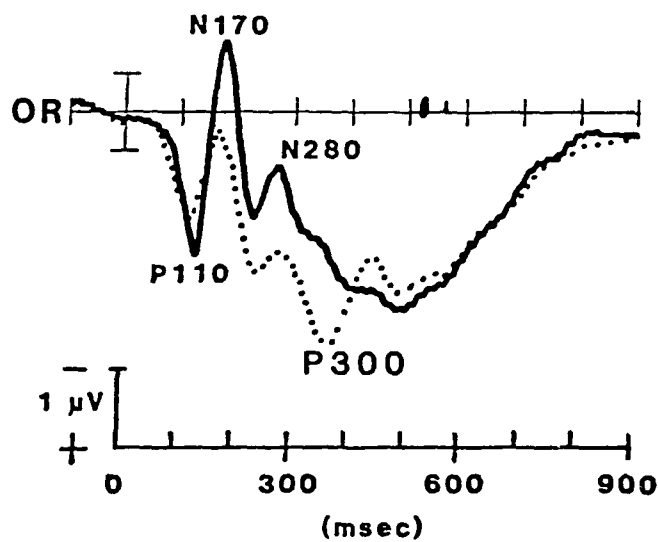
Fig. 8

SIMPLE RT: Central Cue

Fig. 9

ELECTROPHYSIOLOGY OF VISUAL ATTENTION

Steven A. Hillyard, George R. Mangun and Steven J. Luck

Department of Neurosciences

University of California, San Diego

La Jolla, California   92093-0608

and

Hans-Jochen Heinze

Department of Neurology

Medical School of Hannover, FRG

The ability of human observers to deploy their attention
rapidly to the most important parts of a visual scene has impor-
tant consequences for perception. A rapidly expanding research
literature has established that stimuli positioned at or near an
attended location in the visual field are processed more effi-
ciently than are stimuli at some distance from the focus of
attention (for recent reviews see Ericksen and Yeh 1985; Prinzme-
tal et al., 1986). The enhanced processing of attended events
may take the form of improved detectability for faint stimuli,
improved discriminability of stimulus features and patterns, or
speeded motor responses to expected targets. This attentional
process has been likened to a focal "spotlight" or "zoom lens"
that facilitates the processing of stimuli within a circumscribed
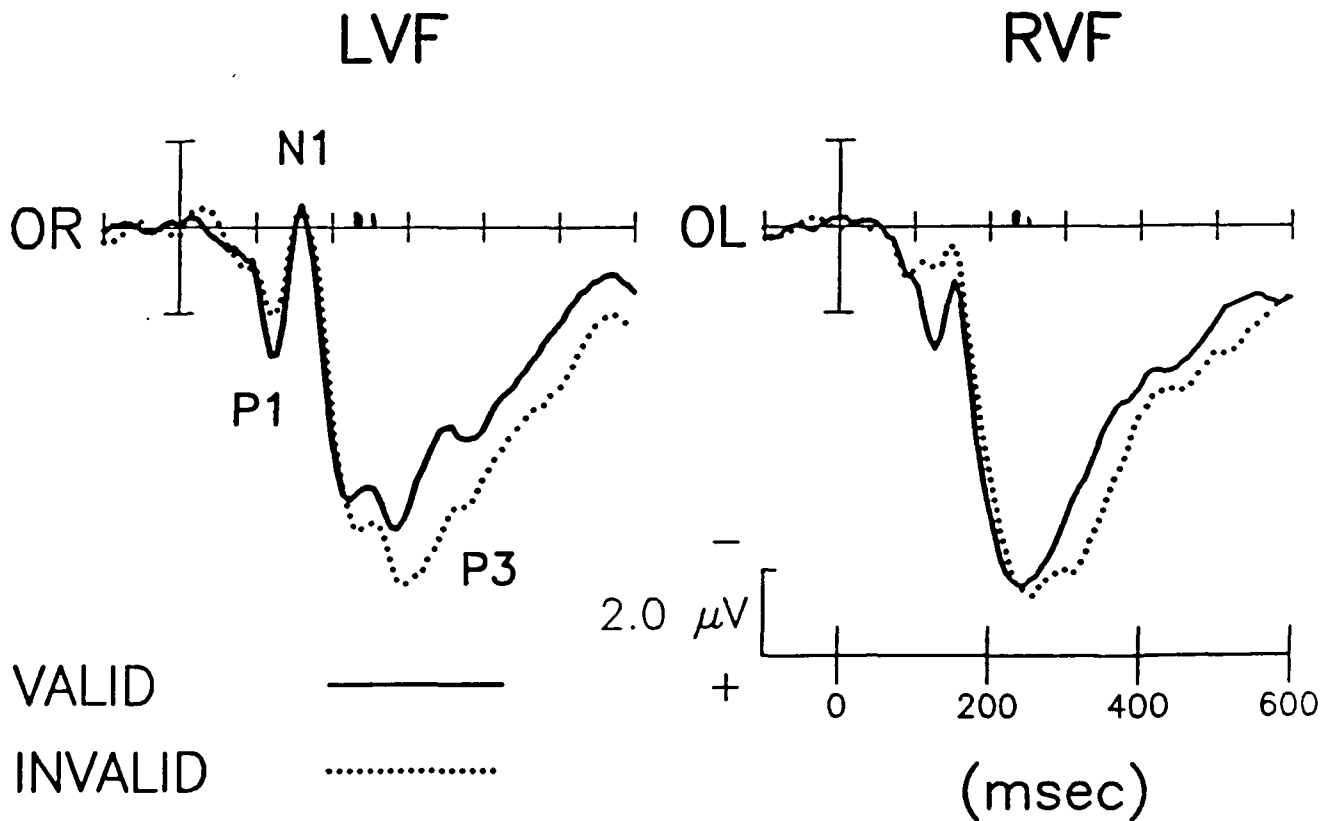zone around the attended locus. In some cases, however, the zone
of facilitation may take the form of a broader "gradient" of
attention that is maximal at the attended location and drops off
gradually across the visual field (e.g., Schulman et al 1986).
These facilitatory effects are not a consequence of eye movements
towards the attended location, which must be strictly controlled
in a proper experimental design.

Despite the recent surge of experimental interest in
visual-spatial attention, many of its fundamental mechanisms
remain poorly understood. At the most basic level, there is a
controversy regarding the extent to which moving attention to a
location results in an actual improvement in the quality of sen-
sory information taken in versus the extent to which it alters
the decision criterion responding to attended or expected events
(Shaw 1984; Sperling 1984). This is a version of the traditional
"early" versus "late" selection issue--does attention actually
modulate the flow of sensory information at a relatively early
level of processing or does it bias higher recognition and deci-
sion systems to favor specific inputs?

Electrophysiological studies in human subjects are playing
an increasing role in the analysis of attentional processes (for
reviews see Harter and Aine 1984; Hillyard and Picton 1987). In
particular, recordings of event-related potentials (ERPs) can
reveal the precise time course of neural events at successive
stages of sensory processing. ERPs are voltage fluctuations
recorded from the scalp that are time-locked to sensory, motor or
cognitive processes and are characterized by particular laten-
cies, polarities, waveshapes and scalp distributions. These vol-
tage fields reflect the synchronous activity of neuronal popula-
tions engaged in information transactions in different brain
regions. Thus, recordings of ERPs to attended and unattended
stimuli can reveal the timing of stimulus selection processes and
provide an indication of the anatomical location of the underly-
ing neuronal processes. During visual-spatial selective atten-
tion, for example, relatively short-latency ERP components (75-
150 msec latency) evoked by attended-location stimuli show

substantial amplitude enhancements at scalp sites that overlie visual cortical areas. Such information has obvious relevance to the question of whether spatial attention improves visual encoding and perceptual accuracy.

ERPs elicited by visual stimuli consist of a series of positive and negative voltage deflections that have characteristic latencies and morphologies (Figure 1). Over posterior scalp these include the P1 (peaking between 100-140 msec), N1 (160-200 msec), P2 (220-250 msec) and N2 (260-300 msec) waves. These ERP peaks are sensitive to the spatial focussing of attention, with attended-location stimuli evoking larger P1, N1, N2 (and sometimes P2) amplitudes, as compared to when attention is directed elsewhere (e.g., Eason et al., 1969; Eason 1981; Harter et al., 1982; Hillyard and Munte 1984; Neville and Lawson 1987; Rugg et al., 1987). The early attention effects on the P1 and N1 waves are manifested as amplitude enhancements of the ERP peaks and are usually largest at scalp sites overlying visual cortex; typically these amplitude modulations do not include any changes in the ERP waveshapes or scalp topographies. Further, the P1 and N1 amplitude changes are essentially equivalent for tasks in which attention is cued to a location on a trial-by-trial basis (Mangun, Hansen and Hillyard 1987) or is sustained at one location throughout a sequence of stimuli (e.g., Hillyard and Munte 1984; Mangun and Hillyard 1988).

This pattern of ERP results is consistent with an attentional mechanism of early sensory gating or "gain control" that is mediated by descending neural influences upon the afferent sensory pathways (Eason 1981; Hillyard and Mangun 1987). This early "gain boost" in the transmission of attended signals presumably underlies the improved perceptual accuracy observed for attended targets and forms at least part of the neural basis of the "attentional spotlight". The precise location in the visual pathway of this selection mechanism is uncertain, but the scalp maximum of the P1 peak (90-140 msec latency) is at lateral occipital scalp sites that approximately overlie extrastriate visual cortical areas 18 and 19 (Mangun and Hillyard 1988; in press).

The early P1 and N1 amplitude modulations are unique to spatial attention. Different patterns of ERP components are found in association with selective attention to other stimulus features such as color, spatial frequency, orientation or shape, as well as various conjunctions of these features. The predominant ERP response to these non-spatial features when attended is a distinctive broad negative component ("selection negativity") beginning at 150-200 msec and extending until 300-400 msec (Harter et al., 1982; Harter and Aine 1984). Interestingly, ERP evidence suggests that selection of features such as color or form appears to be hierarchically dependent upon the prior selection for location (Hillyard and Munte 1984). This capability of

spatially focussed attention to control the analysis of other stimulus features provides strong support for "early selection" models of attention. This result is also in line with recent evidence that spatial attention can gate the registration of simple feature information (Kahneman and Treisman 1984; Prinzmetal et al., 1986).

During both spatial and non-spatial selective attention, the ultimate identification of task-relevant target stimuli triggers a P300 component onsetting at 200-300 msec, which is absent if the target is "missed" (e.g., Coles et al., 1985; Hansen and Hillyard 1983; Donchin et al., 1986; Wijers et al., 1987). Thus, ERPs provide a window into the entire range of early and late stimulus selections throughout the interval 75-300 msec, well before the occurrence of the discriminative motor responses that form the main data base for behavioral investigations.

Current Source Density Analyses

In order to localize the neural generators of attention-sensitive ERP activity more precisely, we have employed two-dimensional current source density (CSD) analysis from multichannel scalp recordings. CSDs can be obtained by placing electrodes in a geometrical grid such that each electrode sits in the center of a square comprised of four neighboring electrodes (i.e., a LaPlacean montage) . By subtracting the average voltage of the four neighboring electrodes from the voltage of the central electrode, an estimate can be obtained of the instantaneous brain electrical current flowing perpendicularly to the scalp at that location (MacKay 1984; Mitzdorf 1985). By mapping the distribution of the perpendicular currents over the electrode array, the neural generators producing the current flows can be localized within the underlying cortical areas. The CSD analysis is better suited to localizing cortical generators than is simple voltage mapping, since the current-flow calculations are reference-free and specifically emphasize superficial rather than deep sources (Srebro 1987; Pernier et al., 1988).

An example of such a CSD mapping is shown in Figure 2 for the P1 component (100-120 msec) elicited by small rectangular flashes of light in the upper left quadrant of the visual field. In this experiment, rectangles were flashed to the four quadrants of the visual fields (c.a. 6 degrees from fixation) in random order at interstimulus intervals of 250-450 msec. The subject's task was to attend selectively to the stimuli at one of the four locations and press a button upon detecting infrequent "target" stimuli (slightly smaller rectangles) at that location. As is usual in this type of experiment, the P1 component showed amplitude enhancement for flashes at attended locations while maintaining its contralateral, posterior scalp distribution (Mangun and Hillyard 1988, in press).

The map on the left side of Figure 2 shows the voltage topography of the P1 wave, and the smaller map on the right shows the topography of the current source density obtained from the 12 LaPlacean montages located over posterior scalp. A sharply focussed current source is seen over the right (contralateral) occipital area, with a smaller source appearing in a mirror image location over the left hemisphere. By relating the scalp electrode sites to underlying cortical areas (Homan et al., 1987) we have suggested that the source for the attention-sensitive P1 wave may be in the lateral pre-striate cortex (Mangun and Hillyard, in press).

In monkeys, the lateral pre-striate cortex contains areas V2, VP, and V4, which analyze form and color information received from striate cortex and project outputs to inferior temporal cortex (DeYoe and Van Essen 1988). There are some intriguing correspondences between the P1 component in humans and neural activity recorded from area V4 in monkeys. The latencies of V4 units in macaques range from 70-90 msec (Robinson and Rugg 1988), which is in line with onset latencies of 80-100 msec (depending on stimulus brightness and eccentricity) for the human P1. In addition, Desimone and associates have found that unit activity in the monkey area V4 (but not V1 or V2) is sensitive to whether or not attention is being paid to the location of the evoking stimulus (Moran and Desimone 1985; Spitzer et al., 1988). On the basis of available scalp recorded data in humans, however, it would be premature to conclude that the P1 component reflects neural activity and attentional control in the human homologue of area V4. It is possible that the attentional control manifested in the P1 over pre-striate areas is actually imposed at an earlier level of the visual pathway (cf. Eason 1981). Further work is required, to bring these lines of research in humans and monkeys together.

Selective Attention to Bilateral Stimulus Arrays

The studies of visual-spatial attention reviewed above and elsewhere in the literature (Harter and Aine 1984; Mangun and Hillyard, in press) all presented random sequences of stimuli, one at a time, to attended and unattended locations. Although paying attention to such stimuli produces robust enhancement of early ERP components (P1 and N1), it is not clear that such conditions are optimal for producing attentional selectivity. Since the appearance of a single stimulus in an otherwise "empty" visual field tends to draw attention to its location whether it is attended or not (Jonides 1981; Posner and Cohen 1984), it is not surprising that a strong selective attentional set may be difficult to maintain when isolated events are regularly presented to unattended locations (Muller and Rabbit 1988).

Behavioral studies have obtained stronger and more consistent attention effects (i.e., differential processing of attended and unattended elements) in situations where a multi-element display (e.g., a ring of letters) is presented, and the subject's attention is pre-cued to one location within the display. Under these conditions, subjects are faster and more accurate at identifying stimuli such as letters in the attended (cued) portion of the display (Jonides 1981; Eriksen and Yeh 1985). Further, it should be noted that multi-element stimulus arrays are more realistic representations of the visual scenes encountered in everyday experience.

In a recent study (Heinze et al. in press), we recorded ERPs to bilateral stimulus arrays and unilateral "probes" presented in a rapid, random sequences while subjects attended exclusively to the right or left visual field portions of the display. ERPs to the bilateral arrays exhibited P1 components of enhanced amplitude over the occipital scalp contralateral to the attended visual field. Such a finding was interpreted as evidence that the visual pathways carrying information from the attended portion of the bilateral arrays were relatively facilitated. These findings established that focal attention within bilateral, multi-element stimulus arrays can be indexed by electrophysiological measures. Further, these data suggest a means by which ERP and behavioral paradigms can be combined to investigate the relationship between ERP amplitude and perceptual sensitivity in a highly focussed attentional task.

Figure 3 illustrates the stimulus sequence used in a subsequent study that was designed to investigate the relationship between ERP amplitudes and perceptual sensitivity (d') during focussed attention within a bilateral stimulus display. Stimuli consisted of a rapidly flashed sequence (350-700 msec ISI) of bilateral arrays of symbols (4.7 deg. eccentricity) that were randomly interspersed with unilateral symbol pairs presented unpredictably to the left or right visual field. A masking stimulus immediately followed the unilateral symbols. While maintaining fixation centrally (verified with EOG and infrared scleral reflective monitoring), subjects were instructed prior to each run to attend exclusively to the left- or right-side pairs of symbols in the bilateral arrays in order to discriminate and memorize the symbols presented on that side. When the unilateral stimulus was flashed (in either visual field), the subjects' task was to determine whether those unilateral symbols were the same (target) or different (non-target) from the symbol pair on the attended side of the immediately preceding array. Subjects indicated targets with a right-hand button press. ERPs and detection scores were obtained for the stimuli separately as a function of attend-left or attend-right condition.

The aim of this study was to create a stable, focussed attentional bias to one-half of the display by requiring

discrimination and memorization of attended-side symbols, and then to compare discrimination accuracy (and its ERP correlates) for the unilateral stimuli falling within versus outside of the focus of attention. Significantly, the design allowed us to assess whether or not the subjects' attention was focussed at the to-be-attended location immediately prior to onset of the unilateral stimulus. This was possible because in order for the subject to identify a unilateral stimulus as a target or non-target they had to know what symbols had preceded it on the attended side. The discrimination of the symbols on one side of the bilateral array was adjusted so as to be too difficult to allow subjects to divide their attention between left and right sides of the display. Thus, if a target was correctly detected we could infer that the subject had been selectively attending to the designated location prior to unilateral stimulus onset.

The effect of lateralized attention in the ERPs to bilateral stimuli was an increase in positivity over the occipital scalp contralateral to the attended visual half-field (p<.01) (Figure 4). The onset of this effect coincided with that of the visual P1 component and the effect was maximal at the occipital scalp sites. Figure 5 shows the ERPs elicited by the unilateral target stimuli that were correctly detected; these data are collapsed over left and right scalp sites to yield waveforms for contralateral and ipsilateral scalp sites relative to stimulus location. Significant attention-related differences included a positive deflection onsetting at 60-80 msec over contralateral occipital scalp sites (p<.01) and an increased negativity in response to attended-side targets over parietal, central and frontal scalp sites bilaterally (p<.01). Attentional difference waves for the unilateral targets were computed by subtracting the unattended ERPs from the attended waveforms (Figure 6). The early attention effect over contralateral occipital scalp is seen to be a broad positivity that continues until approximately 300 msec post-stimulus. Thus, as in the Heinze et al (in press) study, the attention effects for both bilateral and unilateral stimuli appear as positive shifts over contralateral occipital scalp that are not followed at those sites by an N1 attention effect as is typically seen in experiments using randomized sequences of unilateral stimuli.

The target detection measures (d' and beta) are summarized in Figure 7. The d' scores for the unilateral stimuli were significantly higher when they occurred in the attended versus unattended half-field (p<.001). Measures of response criteria tended towards larger values for the unattended-side targets, but this difference did not reach statistical significance (p> .10).

Together, these findings support the hypothesis that spatial selective attention modulates the flow of information in the visual pathways. The ERP data suggest that this effect begins as early as 60-80 msec post-stimulus and is localized over lateral

occipital scalp sites contralateral to the attended stimulus field. These attention-related alterations in sensory processing appear to improve perceptual representations of the attended location stimuli, as reflected in the higher signal detection scores for those events (c.f. Downing 1988).

Selective Attention and Feature Detection

Multi-element stimulus arrays can also be employed to study the effects of spatial selective attention on feature detection. When an object contains a simple visual feature that distin-guishes it from the rest of the visual scene, it appears to "pop out" from the display and can be detected effortlessly. Several authors have suggested that simple features such as color are detected automatically and preattentively, and that this automatic feature detection process may provide the basis for texture segregation (e.g., Julesz, 1984; Treisman & Gelade, 1980). It has proven difficult to assess the automaticity of pop-out detection with behavioral measures, however, because it is usually necessary to make a stimulus task-relevant in order to elicit a behavioral response. The ERP technique can be quite useful in cases such as this, because ERPs allow the assessment of cognitive processing in the absence of any overt responses.

Luck and Hillyard (1988) used ERPs to provide evidence that pop-outs are indeed detected automatically. In this study, sub-jects were presented with arrays of 8 randomly-positioned items, one of which (i.e., the pop-out) differed from the others on 50% of trials. The background items were small, blue, vertical rec-tangles, and the pop-out item differed by virtue of being either green, horizontal, or larger in size. For each block of stimuli, one of the pop-out types was designated the target that required a right hand response and the other two pop-out types were grouped with the no pop-out stimuli as non-targets (left hand response). Despite the fact that the non-target pop-out arrays did not need to be distinguished from the no pop-out arrays, the former elicited a larger N2 wave over anterior electrode sites, as shown in Figure 8. The presence of this anterior N2 provides evidence that a pop-out may register automatically even when its discrimination is not explicitly required. The target arrays elicited both an enhanced anterior N2 and a broadly distributed late positive (P3) component.

An additional experiment was conducted to determine whether the detection of pop-out items can be affected by spatial selec-tive attention (Luck & Hillyard, 1989). In this experiment, the stimulus arrays consisted of 12 randomly-positioned items, 6 in each visual field. As in the previous experiment, the background items were blue vertical rectangles, and a single pop-out item was present on 50% of trials. The pop-out item could be either a green vertical rectangle or a blue horizontal rectangle, and could occur at random on either the left or right side. For each

block of stimuli, one of the two types of pop-out stimuli was
designated relevant, and the subject was instructed to attend to
one side of the display and to respond only when the relevant
pop-out occurred on that side. Each block of trials therefore
contained some arrays with a relevant pop-out item (25%), some
with an irrelevant pop-out item (25%), and some with no pop-out
(50%). In order to increase task difficulty and thereby create a
need for attentional selectivity, the stimuli were presented at a
faster rate than in the previous experiment (750 msec average
interstimulus interval, compared to 1500 msec in Luck and Hill-
yard, 1988).

The effects of spatial selective attention are displayed for
the no pop-out arrays in Figure 9. As in the previously
described experiment (Fig. 4), the bilateral arrays elicited a
broad positivity that was largest at posterior scalp sites con-
tralateral to the attended side; this asymmetry was present for
all stimulus types. The later phase of the attention effect was
more anteriorly distributed than the earlier phase, suggesting
that it may actually consist of two overlapping positive deflec-
tions, the earlier possibly representing a modulation of the exo-
genous P1 wave. In any case, these data indicate that the
attended and unattended sides of the stimulus arrays were dif-
ferentially processed beginning as early as 65 msec post-
stimulus.

A key question in this experiment was whether or not pop-out
stimuli in the unattended field would be discriminated as indexed
by altered ERP components, such as the anterior N2 elicited by
task-irrelevant pop-outs in the previous experiment. As shown in
Figure 10A, the ERP waveform elicited by irrelevant pop-out in
the unattended hemifield is identical to the ERP waveform for the
no pop-out stimulus, while the same irrelevant pop-out stimulus
elicited an enlarged anterior N2 component when it occurred on
the attended side (Figure 10B). This indicates that spatial
selective attention can suppress the processing of task-
irrelevant pop-outs, at least insofar as this processing is
reflected by the anterior N2 component.

One possible explanation for this suppression of pop-out
information would be that stimulus information from the unat-
tended side is suppressed at an early level, to such an extent
that the degraded information is not sufficient for later pro-
cessing systems to detect the pop-out. If this explanation were
correct, then the detection of relevant pop-outs occurring in
unattended locations should have been suppressed as well. How-
ever, relevant pop-outs on the unattended side did elicit an
enlarged anterior N2 component (Figure 10C), indicating that
these pop-outs were detected even though they occurred in an
unattended location. Since an early degradation of information
from the unattended side should have affected both types of pop-
outs, the suppression of the N2 effect only for the irrelevant

pop-out suggests that higher, feature-specific selection processes must be involved as well in detecting the relevant pop-outs.

Considered together, these results indicate that spatial selective attention may affect several levels of visual processing. The existence of an early selection process based on location alone is implicated by the finding that all stimuli elicited a positivity over contralateral visual cortex beginning around 65 msec, regardless of whether the stimulus array contained a pop-out item. As described above (Figure 7), this spatial filtering process may alter the quality of sensory processing for attended versus unattended stimuli, as reflected in the d' measure of perceptual sensitivity. In addition, the presence of an anterior N2 enlargement for relevant, but not irrelevant, pop-outs in the unattended half of the array suggests that higher order feature analyses that lead to pop-out detection may also be affected by attention.

REFERENCES

Coles, M.G.H., G. Gratton, T.R. Bashore, C.W. Eriksen, and E. Donchin. (1985). A psychophysiological investigation of the continuous flow model of human information processing. Journal of Experimental Psychology: Human Perception and Performance, 11, 529-553.

DeYoe, E.A. and D.C. VanEssen. (1988). Concurrent processing streams in monkey visual cortex. Trends in Neuroscience, 11, 219-226.

Donchin, E., D. Karis, T.R. Bashore, M.G.H. Coles, and G. Gratton. (1986). Cognitive psychophysiology and human information processing. In M.G.H. Coles, E. Donchin and S.W. Porges (Ed.), Psychophysiology: Systems, Processes and Applications (pp. 244-267). New York: Guilford Press.

Downing, C.J. (1988). Expectancy and visual-spatial attention: Effects on perceptual quality. Journal of Experimental Psychology and Human Perceptual Performance, 14, 188-202.

Eason, R., M. Harter, and C. White. (1969). Effects of attention and arousal on visually evoked cortical potentials and reaction time in man. Physiology and Behavior, 4, 283-289.

Eason, R.G. (1981). Visual evoked potential correlates of early neural filtering during selective attention. Bulletin of the Psychonomic Society, 18, 203-206.

Eriksen, C.W. and Y.Y. Yeh. (1985). Allocation of attention in the visual field. Journal of Experimental Psychology: Human Perception and Performance, 11, 583-597.

Hansen, J.C. and S.A. Hillyard. (1983). Selective attention to multidimensional auditory stimuli in man. Journal of Experimental Psychology: Human Perception Performance, 9, 1-19.

Harter, M.R., C. Aine, and C. Schroeder. (1982). Hemispheric differences in the neural processing of stimulus location and type: Effects of selective attention on visual evoked potentials. Neuropsychologia, 20, 421-438.

Harter, M.R. and C.J. Aine. (1984). Brain mechanisms of visual selective attention. In R. Parasuraman and D.R. Davies (Ed.), Varieties of Attention (pp. 293-321). Academic Press.

Heinze, H.J., S.J. Luck, G.R. Mangun, and S.A. Hillyard. (In press). Visual event-related potentials index focused attention within bilateral stimulus arrays: I. Evidence for early selection. Electroencephalography and Clinical Neurophysiology.

Hillyard, S.A. and G.R. Mangun. (1987). Commentary: Sensory gating as a physiological mechanism for visual selective attention. In R. Johnson, Jr., J.W. Rohrbaugh and R. Parasuraman (Ed.), (EEG Supplement 40). Current Trends in Event-Related Potential Research (pp. 61-67). Elsevier Publishers.

Hillyard, S.A. and T.F. Munte. (1984). Selective attention to color and locational cues: An analysis with event-related brain potentials. Perception and Psychophysics, 36, 185-198.

Hillyard, S.A., T.F. Munte, and H.J. Neville. (1985). Visual-spatial attention, orienting and brain physiology. In M.I. Posner and O.S. Marin (Ed.), Mechanisms of Attention: Attention and Performance (Vol. XI, pp. 63-84). Hillsdale, New Jersey: Erlbaum Publishers.

Hillyard, S.A. and T.W. Picton. (1987). Electrophysiology of cognition. In F. Plum (Ed.), Handbook of Physiology Higher Functions of the Nervous System Section 1: The Nervous System Vol. V Higher Functions of the Brain, Part 2 (pp. 519-584). American Physiological Society.

Homan, R.W., J. Herman, and P. Purdy. (1987). Cerebral location of international 10-20 system electrode placement. Electroencephalography and Clinical Neurophysiology, 66, 376-382.

Jonides, J. (1981). Voluntary versus automatic control over the mind's eye's movement. In J.B. Long and A.D. Baddeley (Ed.), Attention and Performance (Vol. IX). Hillsdale, New Jersey: Erlbaum.

Julesz, B. (1984). Toward an axiomatic theory of preattentive vision. In G. Edelman, M. Cowan and M.D. Gall (Ed.), Dynamic Aspects of Neocortical Function (pp. 120-148). New York: Wiley.

Kahneman, D. and A. Treisman. (1984). Changing views of attention and automaticity. In R. Parasurman and R. Davies (Ed.), Varieties of Attention (pp. 29-61). London:

Luck, S.J. and S.A. Hillyard. (1988). Event-related potentials to visual "pop-out" stimuli. **Society for Neuroscience Abstracts, 14**, 1013.

Luck, S.J. and S.A. Hillyard. (1989). On the automatic detection of visual popouts (Annual Meeting of the Society for Psycho-physiological Research). New Orleans

MacKay, D.M. (1984). Source-density mapping of human visual receptive fields using scalp electrode. **Experimental Brain Research, 54**, 579-581.

Mangun, G.R., J.C. Hansen, and S.A. Hillyard. (1987). The spatial orienting of attention: Sensory facilitation or response bias? In R. Johnson, Jr., J.W. Rohrbaugh and R. Parasuraman (Ed.), **Current Trends in Event-Related Potential Research** (pp. 118-124). Amsterdam: Elsevier.

Mangun, G.R. and S.A. Hillyard. (1987). The spatial allocation of visual attention as indexed by event-related brain potentials. **Human Factors, 29**, 195-211.

Mangun, G.R. and S.A. Hillyard. (1988). Spatial gradients of visual attention: Behavioral and electrophysiological evidence. **Electroencephalography and Clinical Neurophysiology, 70**, 417-428.

Mangun, G.R. and S.A. Hillyard. (In press). Electrophysiological studies of visual selective attention in humans. In A. Scheibel and A. Wechsler (Ed.), **The Neurobiological Foundations of Higher Cognitive Function**. New York: Guilford Publishers.

Mitzdorf, U. (1985). Current source-density method and application in cat cerebral cortex: Investigation of evoked potentials and EEG phenomena. **Physiological Review, 65**, 37-100.

Moran, J. and R. Desimone. (1985). Selective attention gates visual processing in the extrastriate cortex. **Science, 229**, 782-784.

Muller, H.J. and P.M.A. Rabbit. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. **Journal of Experimental Psychology: Human Perception and Performance, 15**, 315-330.

Neville, H.J. and D. Lawson. (1987). Attention to central and peripheral visual space in a movement detection task. I. Normal hearing adults. **Brain Research, 405**, 253-267.

Pernier, J., F. Perrin, and O. Bertrand. (1988). Scalp current density fields: Concept and properties. Electroencephalography and Clinical Neurophysiology, 69, 385-389.

Posner, M.I. and Y. Cohen. (1984). Components of visual orienting. In H. Bouma and D. Bouwhuis (Ed.), Attention and Performance X, (Vol. 5, pp. 531-556). Hillsdale, New Jersey: Erlbaum and Associates.

Prinzmetal, W., D.E. Presti, and M.I. Posner. (1986). Does attention affect visual feature integration. Journal of Experimental Psychology: Human Perception and Performance, 12, 361-369.

Robinson, D.L. and M.D. Rugg. (1988). Latencies of visually responsive neurons in various regions of the Rhesus monkey brain and their relation to human visual responses. Biological Psychology, 26, 111-116.

Rugg, M.D., A.D. Milner, C.R. Lines, and R. Phalp. (1987). Modulation of visual event-related potentials by spatial and non-spatial visual selective attention. Neuropsychologia, 25, 85-96.

Shaw, M.L. (1984). Division of attention among spatial locations: A fundamental difference between detection of letters and detection of luminance increments. In H. Bouma, and D.G. Bouwhuis (Ed.), Attention and Performance X: Control of Language Processes (pp. 109-121). Hillsdale, New Jersey: Erlbaum.

Sperling, G. (1984). A unified theory of attention and signal detection. In R. Parasuraman and D.R. Davies (Ed.), Varieties of Attention (pp. 103-181). London: Academic Press.

Spitzer, H., R. Desimone, and J. Moran. (1988). Increased attention enhances both behavioral and neuronal performance. Science, 240, 338-340.

Srebro, R. (1987). The topography and scalp potentials evoked by pattern pulse stimuli. Vision Research, 27, 901-914.

Treisman, A.M. and G. Gelade. (1980). A feature-integration theory of attention. Cognitive Psychology, 12, 97-136.

Voorhis", S.T. "Van and S.A. Hillyard. (1977). Visual evoked potentials and selective attention to points in space. Perception and Psychophysics, 22, 54-62.

Wijers, A.A., T. Okita, G. Mulder, L.J.M. Mulder, M.M. Lorist, R. Poiesz, and M.K. Scheffers. (1987). Visual search and spatial attention: ERPs in focussed and divided attention conditions. Biological Psychology, 25, 33-60.

August 30, 1989

FIGURE LEGENDS

Figure 1. ERPs (middle) and topographic voltage maps (bottom) elicited by right visual field stimuli (top) under different conditions of attention. Stimuli were flashed to the right and left visual fields in random order, and the task was to attend selectively to one field at a time in order to detect infrequent targets occurring within the stimulus stream on that side. Fixation was maintained on a central point (+). ERPs to the right stimuli are shown when attended (solid) and unattended (dotted) (stimulus onset at t=0, and tick marks every 100 msec). The early P1 and N1 components were of greater amplitude when the eliciting stimuli were attended. Topographic voltage maps show the P1 (108 msec) scalp distribution over the head when the eliciting stimuli were attended (left side) and when ignored (right side). Note that, the location of the scalp voltage maximum remains over lateral occipital scalp sites contralateral to the visual field of the stimulus. Positive voltages represented by solid and dot-dash lines, negative by dotted, and zero potential by dashed line; each countour represents voltage increment of 0.20 microvolts. The view is from slightly behind and above; thus, the frontal pole is at the top and the inion at the bottom of each "head".

Figure 2. Topographic voltage map of the P1 component elicited by upper left visual field stimuli (left). Data from 29 scalp electrodes were employed using a four-nearest neighbor interpolation algorithm to derive the isopotential contours. The scalp voltage maximum is seen to be over the lateral occipital scalp of the right hemisphere with a weaker second focus visible over the ipsilateral, left occipital scalp. Topographic maps of the CSD are shown at right. CSDs were computed from the voltage data by subtracting the average of the four neighboring electrodes from the value of the central electrode in each of twelve possible LaPlacean electrode montages over posterior scalp. Values are scaled as percent of maximum minus minimum values. The CSD maps show a scalp current source at the same contralateral right occipital site as the voltage maximum, a weaker ipsilateral source, and a current sink located between the two at the midline.

Figure 3. Diagram of the stimulus sequence viewed by the subjects. Bilateral pairs of symbols were flashed (top 3 panels) and interspersed with unilateral pairs of symbols (targets, 4th panel) that were bordered on top and bottom by red rectangles; the unilateral symbols were followed by a mask (5th panel). Subjects were instructed to attend to and discriminate the symbols on one side of the bilateral array for the duration of each run (less than 1 min). Whenever unilateral stimuli were flashed, subjects had to press a button if the unilateral pair was identical to the pair on the attended side of the preceding array. Thus, the unilateral pair in the figure would be a target requiring a

response if the attention condition was "attend left" but not if it was "attend right".

Figure 4. Grand average ERPs (N=8 subjects) to bilateral stimuli under attend left (solid) and attend right (dotted conditions). Recordings are from left (F3, P3, OL) and right (F4, P4, OR) frontal, parietal and occipital scalp sites. Over the right occipital scalp (OR) the P1 component was largest when the subjects attended the left visual field, whereas over left occipital scalp (OL), the P1 was largest when subjects attended the right visual field.

Figure 5. Grand average ERPs (N=8) to unilateral stimuli when subjects attended to the side on which the unilateral stimulus was flashed (solid) and when they attended the opposite side (dotted). ERPs are collapsed across visual field of stimulus and hemisphere of recording to yield contralateral and ipsilateral recordings with respect to visual field of stimulus. The effect of attention was an amplitude enhancement of the occipital P1 component contralaterally and an increase in the frontal and central N150 component bilaterally. No attentional enhancement of the occipital N1 was observed (compare to Figure 1).

Figure 6. Attentional difference waves obtained by subtracting the unattended waveforms from the attended waveforms of Figure 5. The effect of lateralized attention is seen as a broad positive deflection over contralateral occipital scalp. The positivity began at 60-80 msec and continued until after 300 msec. Over ipsilateral occipital scalp the attention effect can be seen as a slow negative deflection that onsets slightly later (c.a. 130 msec).

Figure 7. Bargraphs of d' (top) and Beta (bottom) scores for left and right visual field targets when they occurred on the attended side (striped) and on the unattended side (solid). The d' scores were significantly higher for the detection of unilateral targets flashed to the attended side. Beta scores were not significantly different for attended or unattended sides.

Figure 8. Grand average ERPs (N=12 subjects) elicited by no pop-out (solid), non-target pop-out (dashed), and target pop-out (dotted) stimulus arrays in the experiment of Luck & Hillyard (1988). These ERPs were averaged over left and right frontal electrode sites.
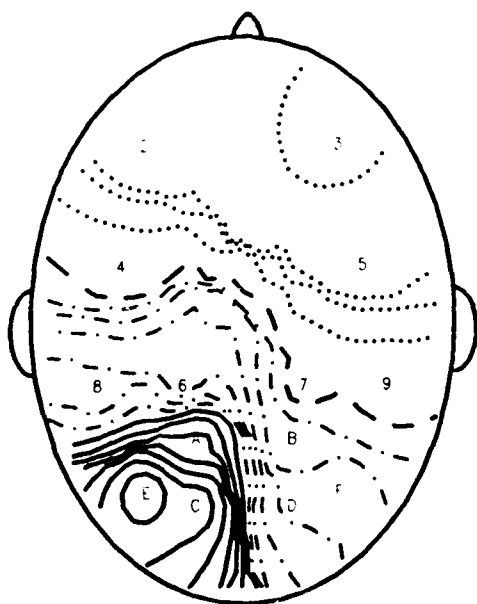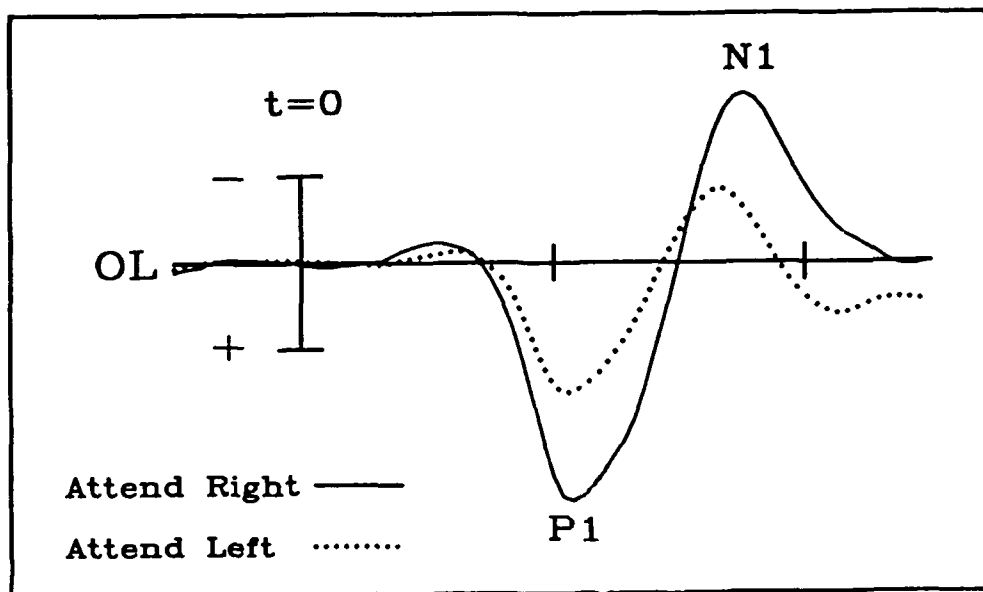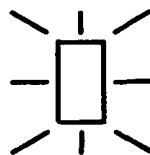
Figure 9. Grand average ERPs (N=12 subjects) elicited by no pop-out stimuli at temporal electrode sites ipsilateral (solid) or contralateral (dashed) to the attended visual field, averaged over attend-left and attend-right conditions (from Luck & Hillyard, 1989).

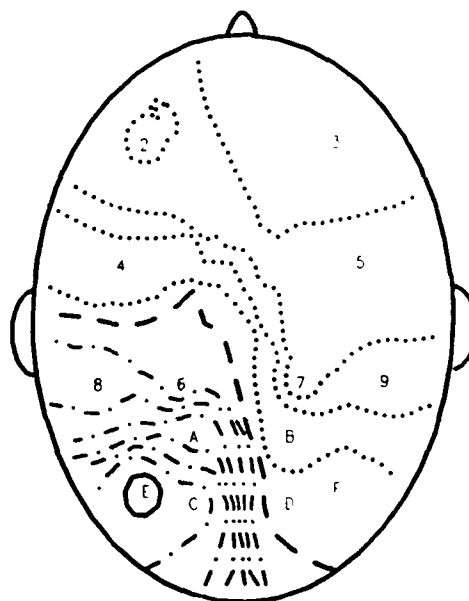Figure 10. Comparison of grand average ERPs elicited by no pop-

out stimuli (solid) and four types of pop-out stimuli (dashed):
A) Irrelevant pop-out on the unattended side; B) Irrelevant pop-
out on the attended side; C) Relevant pop-out on the unattended
side; D) Relevant pop-out on the attended side. These ERPs were
averaged over left and right frontal electrode sites and col-
lapsed across target pop-out type and direction of attention.

N1

t=0

OL

P1

Attend Right ———

Attend Left ....

Attend Right   Attend Left

Fig. 1

P1 TOPOGRAPHY LEFT STANDARDS (108 ms)

% MAX — MIN

————	100.00
————	95.00
————	90.00
————	85.00
————	80.00
————	75.00
————	70.00
– – – –	65.00
– – – –	60.00
– – – –	55.00
– – – –	50.00
– – – –	45.00
– – – –	40.00
· · · ·	35.00
· · · ·	30.00
· · · ·	25.00
· · · ·	20.00
· · · ·	15.00
· · · ·	10.00
· · · ·	5.00
· · · ·	0.00

Voltage

CSD

Fig. 2

Target

Mask

Fig. 3

ERPS TO BILATERAL STIMULI

Attend Left ——————

Attend Right ··············

2.0 μV

0   100   200   300
(msec)
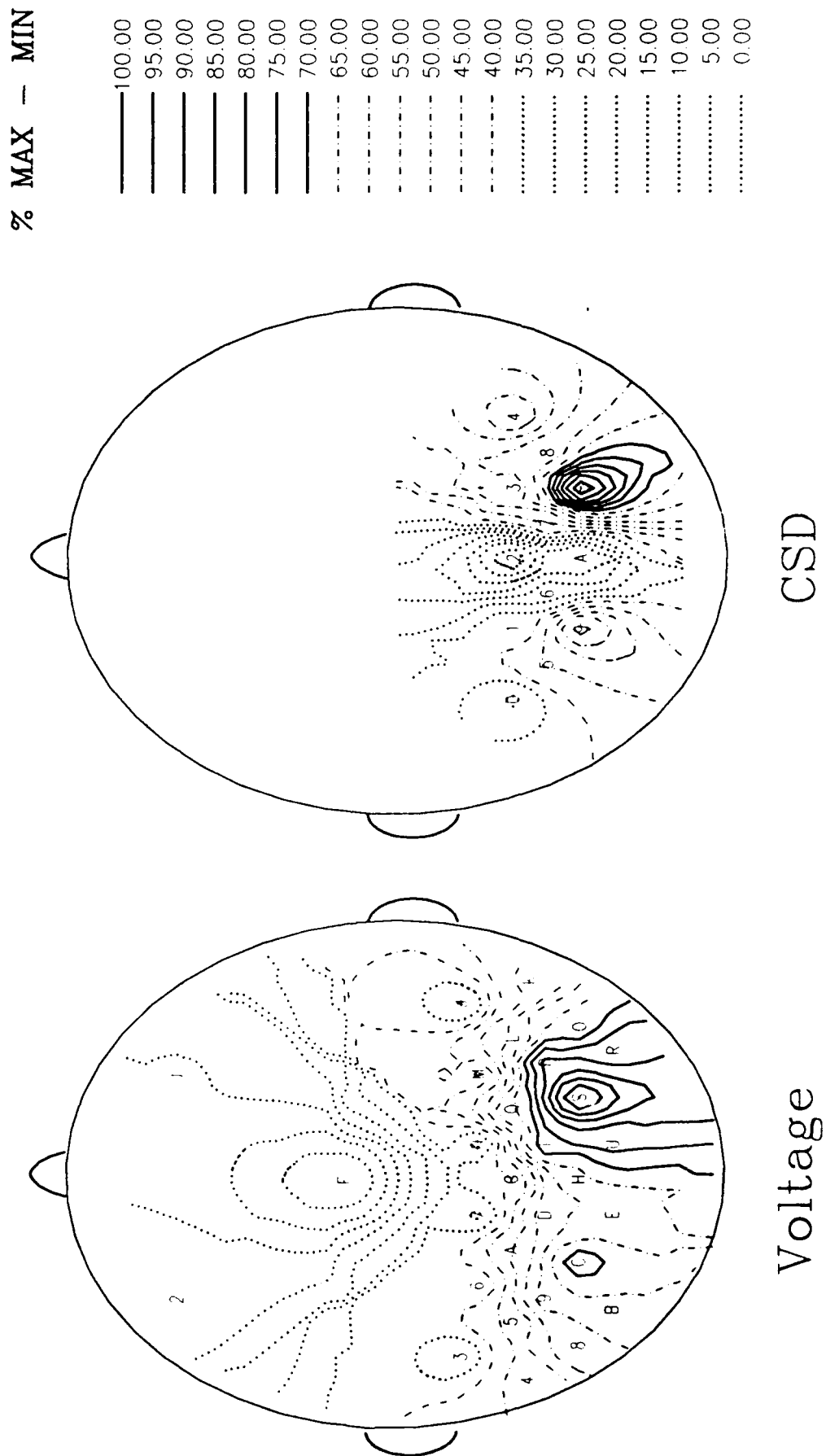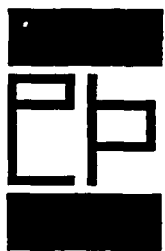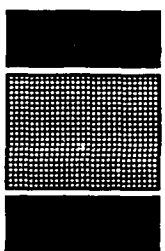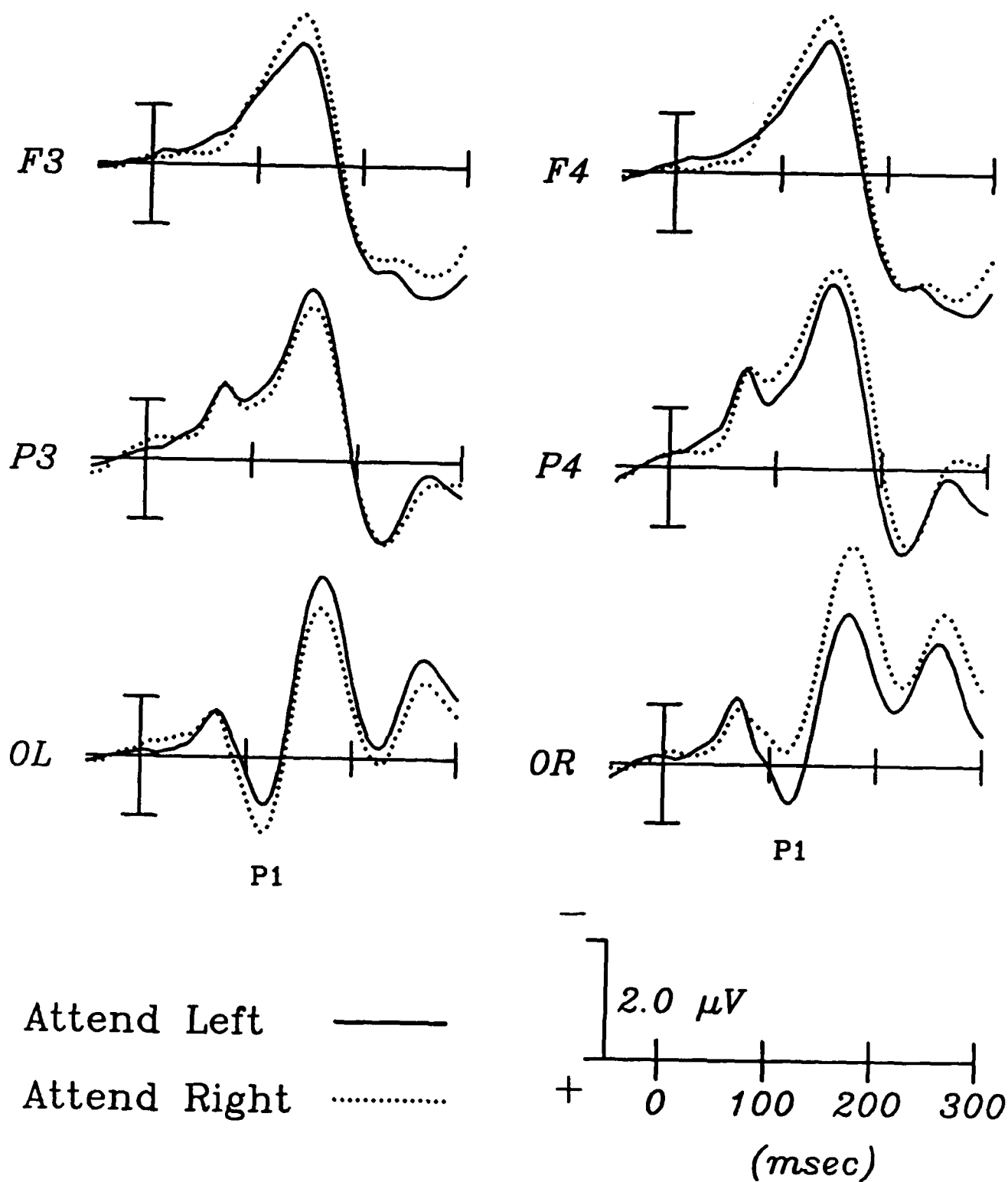
Fig. 4

ERPS TO UNILATERAL TARGET HITS
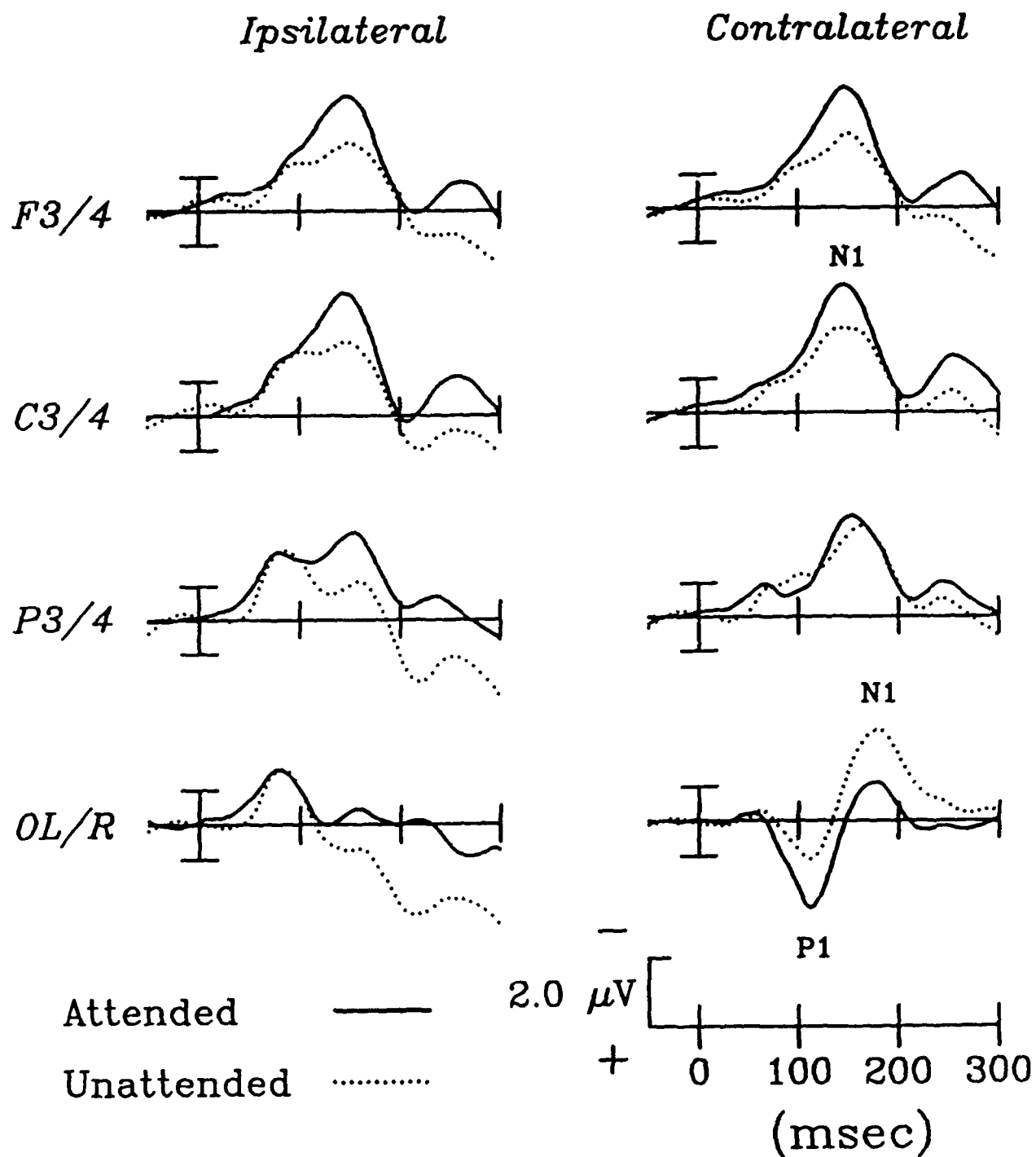
Fig. 5

ATTENTION DIFFERENCE WAVES

Ipsilateral *Contralateral*

F3/4

C3/4

P3/4

OL/R

2 *microvolts*

0   100 200 300
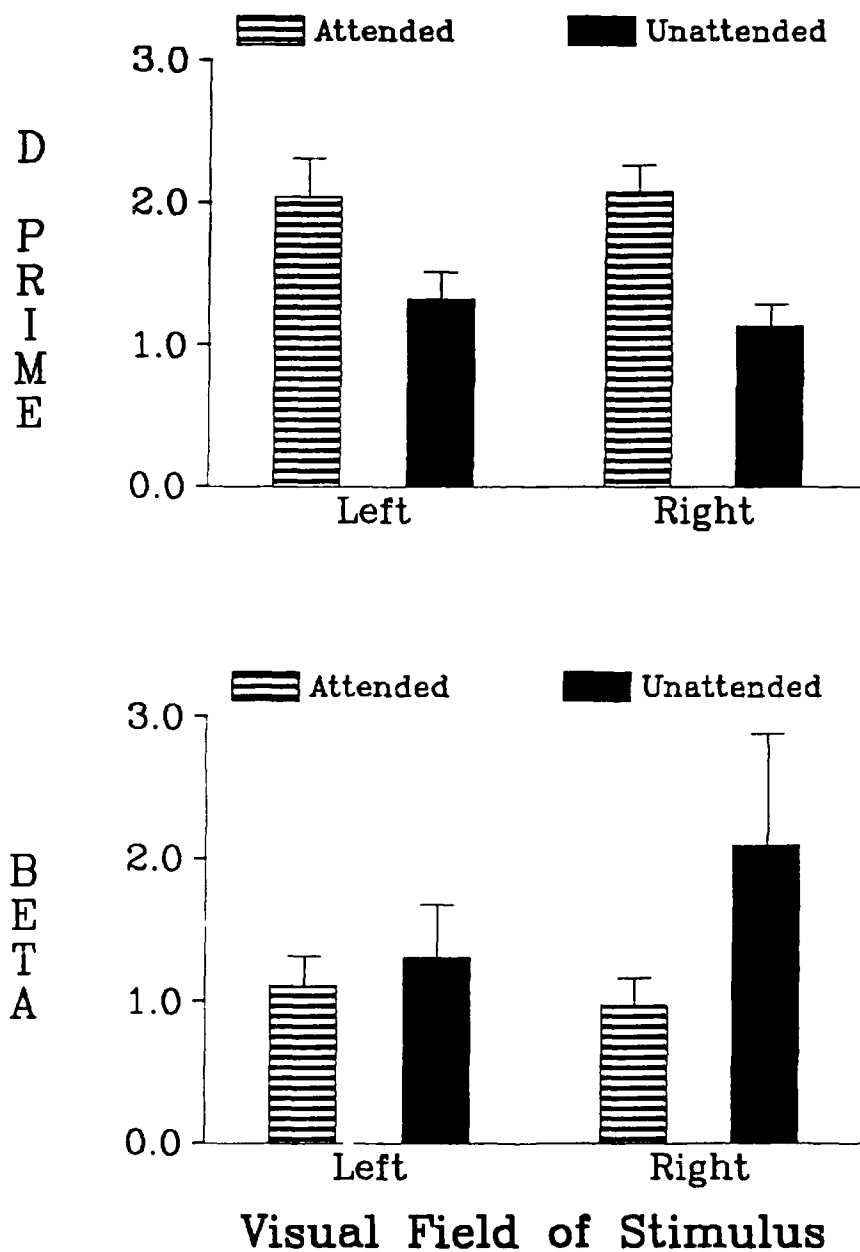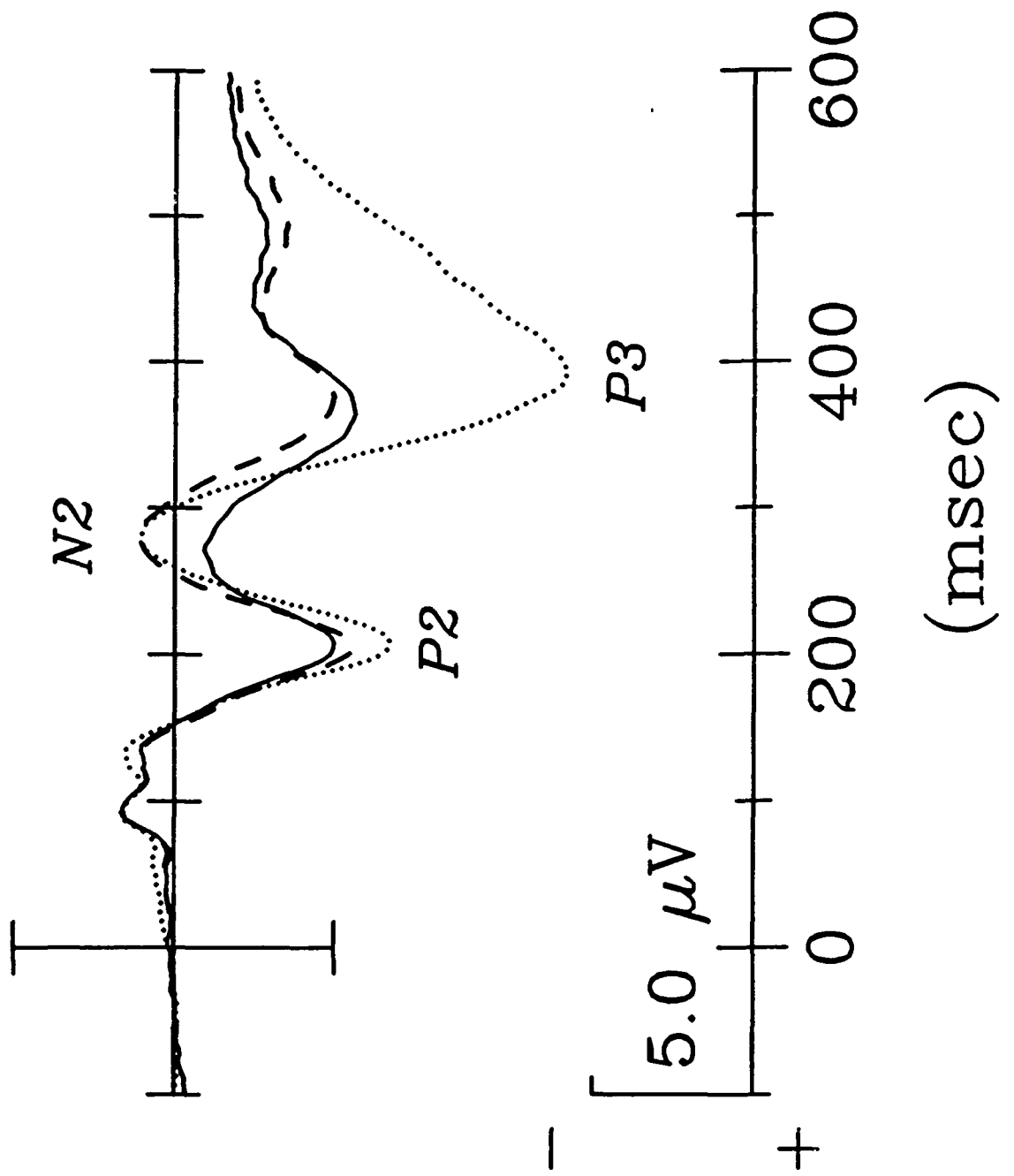
(msec)

Fig. 6

Fig. 7

N2

P2

P3

5.0 μV

$-$

$+$

0　　　200　　　400　　　600

(msec)

Fig. 8

Fig. 9

Fig. 10